VOLUME 8 MAY 1939 No. 1

THE FLOOD FACTOR IN THE ECOLOGY OF CAVES

By R. S. HAWES

From the Zoology Department, King's College, University of London

EXCEPT, perhaps, for the depths of the sea, the large subterranean cave is usually supposed to be the least changeable of all animal habitats, its consistently monotonous factors including a low and almost constant temperature, an atmosphere continuously saturated with water vapour, and permanent darkness. Such an introduction is a commonplace of the textbooks, and, on the whole, what it says is true. The caves of the Istrian and Dinaric karst[1] certainly provide a good many illustrations of the conventional account. For example, Kenk & Seliškar (1931) found the maximum and minimum temperatures of water well inside Podpeška jama to be 9·7 and 9·05° C. over two years: the consistently high humidity is shown by the prevalence of Tettigoniidae such as *Dolichopoda* spp. which can live only in this damp atmosphere (Chopard, 1932): and, of course, the caves are dark.

Clearly, however, the constant effect of these factors may be greatly weakened by the operation of any seasonal variable affecting the animal community. The purpose of these field notes is to draw attention to seasonal variation in caves caused by flooding, a regular feature of the area described. Flooding occurs rather suddenly, so that there is a sharp distinction between conditions in winter, when the caves are under water, and in summer, when they are merely damp. The results include the imposition on the animals of a biological rhythm—a phenomenon contrary to all that we expect of the "constant" cave environment. In addition, floods may operate as agents of distribution; they help in maintaining a regular food supply to caves; and, as mechanical agents, they introduce species from above ground and so initiate colonization.

Popovopolje, in Herzegowina, lies parallel with the Adriatic Sea. It is a typical "polje",[2] about 50 km. long and from 2 to 7 km. wide. In summer, the fertile floor is cultivated. It is surrounded on both sides by dry, barren limestone hills, renowned for their caves. The caves investigated all lie within

[1] Much of Jugo-Slavia consists of the Cretaceous limestone formation called karst, i.e. a barren, rather desolate, countryside, in summer very dry, riddled with caves and with more permanent water below than above ground.

[2] According to J. Cjivić, early in the history of karst formation, surface drainage gave rise to wide, shallow river canyons. When the soil became porous, the drainage became subteranneau, and the abandoned river bed is the polje of the present day. Low lying and damp, the verdant polje contrasts strongly with the surrounding barren country of the typical karst.

about 8 km. of the village of Zavala and hold some of the most remarkable and highly specialized, as well as the rarest, of cavicolous species. Vjetrenica pećina, for example, the largest cave in south-eastern Europe, is the home of the blind prawn, *Troglocaris*, the blind Mysid, *Troglomysis* (Stammer, 1933), and of the giant white Amphipods, *Niphargus* (= *Stygodytes*) *balcanicus* and *Metohia carinata* (Absolon, 1927). The cavicolous Urodele Amphibian, *Proteus anguineus*, although rare, also occurs as far south as this.

At all times of the year there is, in some of the caves, a good deal of water, and some, too, are connected by permanent and well-defined underground rivers. Typically, in summer, the walls and floors are damp, except where pools or lakes occur. But in winter, after heavy rains, the underground rivers swell, and pour out of the caves to flood the polje; the mouths of the caves opening at the margins of the polje are themselves submerged, so that, when the waters turn back, whirlpools are created. The peasants at these times cross their own maize fields by boat. Obviously, this violent periodic disturbance must have important ecological effects, and these are most likely to be surprising within the caves, because, in other respects, the cave environment tends to be constant. I have grouped the kinds of effects obtained under three headings. The examples are chosen because they are fairly easy to study, and are suitable for discussion in an introductory sketch of this sort.

(1) *The annual rhythm.* This unexpected and interesting effect may be illustrated by a cave, known as Crnulja, not far from Turković. This is one of the very few known habitats of the Serpulid polychaete worm, *Marifugia cavatica* (Absolon and Hrabě, 1930), which is to be found, in places, in such dense profusion that walls, ceiling and floor are completely covered by huge masses of the tiny, calcareous tubes. For most of the year, the tubes are out of water, the worms withdrawn and covered by a thin film of water of condensation. As is well known, the Serpulidae are characteristically marine animals and very few indeed (e.g. *Mercierella* in Europe) are known outside the sea. It is therefore somewhat astonishing to find a fresh-water Serpulid confined to a cave and living most of its life out of water. How the creature feeds during the dry months is completely unknown.

In the same cave occur a Plumatellid, noted by Remy (1937), who found it in August 1936 in a desiccated condition and stuffed with statoblasts, and a sponge, *Ephydatia mülleri* Lieberkühn, whose gemmules I discovered among the worm tubes a year later. The ordinary sponge gemmule germinates in spring, stimulated probably by a rise in temperature: this stimulus can be used to induce germination artificially at any time of the year (Brien, 1932). But the cavicolous strain must germinate in winter, the only time when the flood water is available, and it is highly probable that this water is colder than the air in which the gemmules have been lying. I was able to show that gemmules from Crnulja do not respond to temperatures which stimulate epigean forms (Hawes, 1938), and it seems reasonable to relate this reversal of the

temperature reaction to the demands on the animal made by periodic flooding. There are thus three fresh-water species belonging to predominantly marine groups characterized by free-swimming ciliated larvae, so that sexual reproduction must be confined to the wet months. Alternate drought and flood impose on these organisms a regular alternation of quiescent and active phases.

(2) *The food problem.* Since caves are dark and animals ultimately depend for their food on green plants, all cavicolous food chains must include some link with the outside world. The colonies of coprophagous beetles living on bat dung in the cave are a good example (Jeannel, 1926). The retreat of the flood waters through caves from the open polje is another such link, and probably the most useful importation here is wood. Nearly all the caves contained some wood, often in great quantity, very rotten and covered with fungi. It was noticeable that pieces of wood were centres of attraction for many animals, especially Collembola, also Thysanura and Isopoda (particularly *Titanethes* spp.) and occasionally Phalangida and Pseudoscorpionida.

Though floods introduce food into caves, the final supply to aquatic animals is not insured. After the recession of the floods, a population previously distributed throughout a relatively large volume of water may be confined to numbers of shallow and more or less isolated pools for as long as eight or nine months. If the pools are close together, as they often are, Amphipods such as *Niphargus* may wriggle from one to another, so that isolation is imperfect. The Entomostraca of the mud bottoms no doubt contribute importantly to the economy of the pool population. But some observed cases evade these suggestions. One pool, about 2 by 1 m. and 6 cm. deep, contained a score each of the large and active Crustacea, *Troglocaris* and *Niphargus balcanicus*. These animals were quite isolated and must have been at least eight months out of reach of an external food supply.

(3) *Colonization.* We may consider flooding (*a*) as a means of passively transferring already cavicolous animals from one cave to another and (*b*) as effecting initial colonization of a cave by previously epigean species. There is no need to dwell on the mechanism by which an animal may be washed out of one and into another cave, but the second point calls for more attention.

How animals came to be in caves at all has been the subject of much conjecture. The following account of the habits of *Paraphoxinus* indicates one approach to the problem.[1] This small Cyprinid fish is, apart from one Spanish species, confined to the Balkans. It is most commonly found in caves, but where there exists a permanent communication between subterranean and surface waters it often occurs in the latter all the year round. Elsewhere, the fish spend most of their time underground, but the floods wash them out in such great quantities and so regularly that the peasants know when and

[1] I am indebted to Dr E. Trewavas for some help with cave fish, but it does not necessarily follow that she lends her authority to my opinions. For a general account of *Paraphoxinus*, see Spandl (1926).

where to look for them and have designed a special method for collecting the catch. Breeding occurs at this time, and the young fish are left to pass a year in the open, though their parents are carried back into the caves. (Possibly the eggs are laid in protected, shallow water, and there they stay, while the older, active fish get involved in the main stream of receding water.) After the next flood, the young fish in turn are swept into the caves. The question is—Are we dealing with a cave dweller which is occasionally washed into the open, or with an essentially epigean fish which is having a cavicolous habit forced upon it? The latter seems to me to be nearer the truth. *Paraphoxinus* occurs above the ground at all times of the year when the opportunity exists. Where it lives mainly in caves it does so because, for most of the year, the only available water is underground. It breeds above ground, and it seems to be unaffected by a change of environment which would act disadvantageously on a more typical cavicolous form thus extracted from its peculiar home.

Is there any evidence that the compulsory adoption of a cavicolous environment is having any effect on *Paraphoxinus*? Its eyes are normal; the suggestion that they are rudimentary (Apfelbeck, 1895) is quite without foundation. But the fish exhibits one character, a tendency to reduced scales, which is remarkably common among cave fishes in general. The reason for this character seems not to be understood—possibly it has to do with increased sensitivity of the skin—but it is certainly very prevalent. Cave fishes are commonly derived from families in which the scales are reduced or absent, e.g. catfish, or the Brotulids of Cuba. Or, if they are members of scaly families, they may independently reduce or lose their scales, e.g. *Barbus* has large scales but, of its cavicolous derivatives, *Caecobarbus* has somewhat reduced scales and *Phraeactichthys* has lost them entirely (Norman, 1926). The genus *Paraphoxinus* is distinguished by the reduction of its scales from the related *Phoxinella*. Are we not justified, then, in concluding that we are here watching the early stages of the colonization of caves by an epigean fish, already beginning to show a typical cavicolous character, and that the responsible agent is flooding?

Summary

1. Although our conception of the persistent constancy of the cave environment may be confirmed again and again by measurements of temperature, humidity and light, the conception is upset by a study of flooding.

2. In a fairly small area of Herzegowina it was found that there was a regular alternation of summer drought and winter flood.

3. This alternation may impose on the animals living in the affected caves a recurrent cycle, in which a quiescent and an active phase regularly succeed each other.

4. Merely as a mechanical agent, flooding plays an important part in maintaining the food supply to caves; within the caves, the recession of the

waters may create special food problems by isolating animals for long periods in small pools.

5. By carrying animals from one to another cave, flooding accounts for certain facts of local distribution. An example is given to show how flooding may act as the cause of initial colonization of a cave by an originally epigean species of fish.

Acknowledgements

I wish to express my thanks to the Trustees of the Godman Exploration and Percy Sladen Memorial Funds for the financial support which they gave to my share of the work on the expedition to Jugo-Slavia; to Prof. Jovan Hadži and Prof. Roman Kenk for their kindness at the Univerza Kralje Aleksandra I, Ljubljana; and to the Director and Staff of the Oceanografski Institut, Split, for help there. I am indebted to Mr R. A. Beatty, with whom I worked in the field, for many useful suggestions, and to Dr C. F. Robinow for much help with the sponge gemmules. And I am especially grateful to Prof. D. L. Mackinnon for her encouragement and advice at all stages of this work.

References

Absolon, K. (1927). "Les grands Amphipodes aveugles dans les grottes Balkaniques." C.R. Assoc. Franç. Avanc. Sci. 51e Session: 291–5.

Absolon, K. & Hrabě, S. (1930). "Über einen neuen Süsswasser-Polychaeten aus den Höhlengewässern der Herzegowina." Zool. Anz. 88: 249–64.

Apfelbeck, V. (1895). "Sur la faune des cavernes de Bosnie et d'Herzégovine." Bull. Soc. Spéléologie (Spelunca), Paris, 1: 23–4.

Brien, P. (1932). "Contribution à l'étude de la régénération naturelle chez les Spongillidae *Spongilla lacustris* (L.); *Ephydatia fluviatilis* (L.)." Arch. Zool. Exp. Gén. 74: 461–506.

Chopard, L. (1932). "Les Orthoptères cavernicoles de la faune paléarctique." Arch. Zool. Exp. Gén. 74: 263–86.

Hawes, R. S. (1938). "Effect on organisms of summer drought in caves." Nature, Lond. 141: 607.

Jeannel, R. (1926). "Faune cavernicole de la France avec une étude des conditions d'existence dans le domaine souterrain." Paris.

Kenk, R. & Seliškar, A. (1931). "Študije o ekologiji jamskih živali. No. 1." [Studies in the ecology of the fauna of caves.] Prirod. Razpr. 1: 5–24. (In Slovenian, with French summary.)

Norman, J. R. (1926). "A new blind catfish from Trinidad, with a list of blind cave-fishes." Ann. Mag. Nat. Hist. Ser. 9, 18: 324–31.

Remy, P. (1937). "Sur *Marifugia cavatica* Absolon et Hrabě, Serpulide des eaux douces souterraines du Karst Adriatique." Bull. Mus. Hist. Nat. Paris, 9: 66–72.

Spandl, H. (1926). "Die Tierwelt der unterirdischen Gewässer." Vienna.

THE DISTRIBUTION OF WILD DEER IN ENGLAND AND WALES

By WILLIAM LING TAYLOR

Observation extending over the past twenty-five years forces the conclusion that in many parts of the country the population of deer at large in a wild state was considerably greater and more widespread in the early years of the present century than was generally recognized. Evidence has since been accumulating that numbers are tending to increase. Forest Officers in charge of the lands acquired by the Forestry Commission in England and Wales since the passing of the Forestry Act, 1919, which now extend to 568,700 acres, have had exceptional opportunities of noting the distribution of the various species of wild deer and their density on the ground. Inspections covering many thousands of acres of privately owned woodlands confirm the experience recorded and there are few of the more densely wooded districts in which deer of one kind or another are not present.

The species native to Great Britain are the red deer (*Cervus elaphus*) and the roe deer (*Capreolus capreolus*). The status of the fallow deer (*Dama dama*) is not so clear, but it has unquestionably been resident in England for a long period, chiefly within the confines of deer parks, but at large elsewhere, as in New Forest and in the Forest of Dean until 1874, from times concerning which no precise information is available. Other species have been introduced into parks and enclosures in more recent years. Individual specimens of these have escaped from time to time and have established themselves as breeding species in those parts of the country in which the escapes have occurred and from which the deer have spread and found sanctuary. Japanese deer (*Sika nippon*), the Chinese muntjac or barking deer (*Muntiacus reevesi*) and the Siberian roe (*Capreolus pygargus*) have been added to the wild fauna of Britain. All three, particularly the Japanese deer, are tending to increase their range and numbers. The Siberian roe and the Chinese muntjac appear at present to be the most strictly localized of the introduced species. It is possible that other exotic deer are at large in small numbers, but none is recorded as having acclimatized itself in or about the newly formed forests or the older Crown Woods.

Deer are woodland animals and conditions to the south of the Scottish border appear to suit them well. The truly indigenous red deer (*Cervus elaphus*) has never been exterminated from West Somerset and Devon where it is still numerous. Wild red deer also occur on the eastern side of the Lake District of Cumberland, Westmorland and North Lancashire, in the New Forest and in a semi-wild state in Savernake Forest in Wiltshire. Where they are to be found at large in other parts of England and Wales they appear to be the

progeny of escapes from enclosed private herds. The wild red deer has survived because of its value for hunting and stalking, and its continuation in its remaining strongholds is due to the considerable degree of protection that has been extended to the species. In its true woodland habitat the red deer is a magnificent and conspicuous animal and if all protection were withdrawn its final suppression in England and Wales could only be a matter of time.

The roe-deer (*Capreolus capreolus*), which is the most truly feral in its habits of all our wild deer, occurs in Northumberland, Cumberland and the Lake District at least as far south as Morecambe Bay. It is established also in the eastern midlands and more strongly in the south of England, particularly in Dorset, Hampshire, Surrey and Sussex. It is numerous in East Anglia in the neighbourhood of Thetford and Brandon as a result of an introduction of some forty or more years ago.

The range of the roe is enlarging both in the north, south and east and, as it breeds freely and is small and well equipped to take care of itself, it is increasing its numbers and in some localities is multiplying with considerable rapidity. It is unquestionable that the afforestation of large areas is aiding this species and, on occasion, numbers have here and there to be reduced; but it is also without question that the roe, which can maintain itself in the face of enclosure and agricultural development without artificial aid, is likely to continue to do so all the more with the additional shelter afforded by the recent afforestations. A very little consideration of the circumstances in which this animal has survived will clearly indicate that of the larger members of the British fauna none is more secure from extinction under existing circumstances than the roe-deer.

The position of the fallow deer (*Dama dama*) is different. The stock from which the fallow deer now at large about the countryside have been drawn is chiefly escaped animals from the herds in the deer parks that still remain as part of the demesnes of many private estates. Possible exceptions occur in New Forest where wild fallow deer are still plentiful, and where record of the origin of the stock has been lost, and on Cannock Chase in Staffordshire. The herd of fallow deer in Savernake Forest and neighbourhood is doubtless also of ancient origin. The fallow deer in the Forest of Dean in Gloucestershire have completely disappeared in that area. An Act of 1668 (20 Carolus II, cap. 8) provides that for the prevention of destruction to young wood by overcharging the Forest with deer not more than 800 deer of all sorts may be kept in the Forest at any one time. In 1849 it is known that there were about 400 deer left, but by 1874 the old stock of fallow deer had all gone. There remains no local recollection of deer of other species than fallow and no deer of any kind are now left in the Forest of Dean, but there is a small herd of fallow deer in the adjacent Highmeadow Woods. Fallow deer running wild occur in large or small numbers in many other districts, notably, as regards numbers, on the Welsh borders of Herefordshire and South Shropshire, in

Nottinghamshire, in parts of Kent, Surrey and Sussex and in Wiltshire and Hampshire. Speaking generally, this species is the most widely and evenly distributed of all wild deer in England and Wales.

The Japanese deer (*Sika nippon*) has established itself in east Dorset and in the New Forest. It is also reported from east Kent and is probably to be found elsewhere. The Chinese muntjac (*Muntiacus reevesi*) is making its way into the woodlands of Bedfordshire and Northamptonshire. The Siberian roe (*Capreolus pygargus*) also occurs at large in the same parts of the country.

Deer in Great Britain have few, if any, natural enemies. Foxes may take a few of the calves and fawns on occasion, but for the rest almost the only dangers come from man. Where deer are plentiful, they are a source of loss to the farmer and to the forester and in excessive numbers are unlikely to be tolerated. Recently wild deer have been suspected as carriers of foot-and-mouth disease and some efforts to suppress them have resulted. In moderate numbers they do little harm and can be an interesting addition to the amenities of the countryside, also, as in the case of the red deer, an attraction to the sportsman. Numbers, however, are not always easy to control. The Deer Destruction Act of 1851 (14 and 15 Vict. c. 76), which applied to the New Forest, resulted in a determined effort to exterminate the deer in that area but the effort proved abortive and there are probably almost as many red, fallow and roe deer in the New Forest to-day as ever there were; the deer population of the New Forest has also been augmented by the more recent invasion of Japanese deer from east Dorset. In those parts of the country which are already populated by deer these animals may quite easily become a problem, for inevitably someone must pay for their keep, either directly or indirectly, and in some localities they are already a nuisance to husbandry.

The following list has been compiled from reports of observations made by the Forestry Commissioners' Officers in England and Wales over the period extending from the passing of the Forestry Act, 1919 to 1938. It does not purport to be an exhaustive record of the present distribution of the various species of wild deer, but it gives an indication of the widely spread areas over which deer occur, and of their relative local abundance:

County	Forest area	Species	Density
Northumberland	Kielder	Roe	Numerous
	Redesdale	,,	Not numerous
	Harwood	,,	Numerous
	Rothbury	,,	,,
	,,	Fallow	Not numerous
Cumberland	Kershope	Roe	,,
Durham	Chopwell	,,	,,
	,,	Fallow	Occasional
	Hamsterley	,,	,,
Lancashire (Furness)	Grizedale	Red	Numerous
	,,	Roe	,,
Yorkshire	Allerston	Fallow	Occasional
Nottinghamshire	Clipstone	,,	Numerous
Lincolnshire	Bourne	,,	Not numerous
	Kirby Underwood	,,	,,

County	Forest area	Species	Density
Staffordshire	Cannock	Fallow	Numerous
Shropshire	Mortimer	,,	,,
Worcestershire	Wyre	,,	,,
Herefordshire	Haugh	,,	,,
Northamptonshire	Hazelborough	Siberian roe	Not numerous
	Salcey	,,	,,
	Fineshade	Fallow	,,
	Fermyn	,,	Numerous
	Yardley	,,	,,
	,,	Siberian roe	Not numerous
Rutland	Pickworth	Roe	Numerous
Norfolk	Thetford	,,	,,
	Harling	Fallow	Not numerous
Suffolk	Brandon	Roe	Numerous
	Mildenhall	,,	,,
	King's Forest (Culford)	,,	,,
	Rendlesham	Fallow	Not numerous
Bedfordshire	Ampthill	Chinese muntjac	,,
	,,	Siberian roe	,,
Gloucestershire	Highmeadow	Fallow	,,
Kent	Hemsted	Unidentified	,,
	Challock	Fallow	Numerous
	,,	Japanese	,,
Sussex	Buriton	Unidentified (more than one species)	Not numerous
	Goodwood	Roe	,,
	,,	Fallow	,,
	Marden	,,	Numerous
Surrey	Chiddingfold	Roe	,,
Hampshire	New Forest	Red	,,
	,,	Roe	,,
	,,	Fallow	,,
	,,	Japanese	,,
	Ringwood	Roe	Not numerous
	,,	Fallow	Occasional
	Alice Holt	,,	Not numerous
	Bramshill	,,	,,
Wiltshire	Gardiner	Roe	,,
	Westwoods	Fallow[1]	,,
Dorset	Puddletown	Roe	Numerous
	Wareham	,,	Not numerous
	,,	Fallow	Occasional
	,,	Japanese	Not numerous
Somerset	Quantocks	Red	Numerous
	Bruton	Fallow	Occasional
Devon	Brendon	Red	Numerous
	Dartmoor	,,	Occasional
	Eggesford	,,	,,
	Okehampton	,,	,,
	Haldon	,,	Not numerous
	Halwill	Fallow	,,
	Lydford	Red	Occasional
Cornwall	Bodmin	,,	Not numerous
	,,	Fallow	Occasional
Caernarvon	Gwydyr	Roe	,,
Merioneth	Coed-y-Brenin (Dolgelley)	Fallow (?)	,,
	Cynwyd	Unidentified	,,
Montgomery	Kerry	Fallow	,,
Carmarthen	Brechfa	Unidentified	,,

[1] Red deer also reported.

THE HABITAT, DISTRIBUTION AND DISPERSAL OF THE PSYCHID MOTH, *LUFFIA FERCHAULTELLA*, IN ENGLAND AND WALES

By RICHARD S. McDONOGH

(*With* 3 *Figures in the Text*)

CONTENTS

	PAGE
1. Introduction	10
2. Habitat:	
(*a*) Local distribution:	
(1) Lichen	11
(2) Species of tree	13
(3) Position of tree	14
(4) Age of tree and its isolation	15
(*b*) Distribution of larvae and pupae on the tree	15
(*c*) Effect of light intensity	16
3. Distribution in England	18
4. Dispersal:	
(*a*) From tree to tree:	
(1) Method of dispersal	22
(3) Rate of colonization	23
(3) Distance covered	24
(*b*) Migrations on the tree	24
(*c*) Factors affecting the activity of the larvae:	
(1) Temperature and humidity	25
(2) Light	26
(3) Geotropism	27
5. Summary	27
References	28

1. Introduction

This paper is part of the results of a biological investigation of the small Psychid moth *Luffia ferchaultella* (Stephens). The species is parthenogenetic and wingless. The larvae are case-bearers and live on tree trunks and sometimes on stones (e.g. at Stonehenge), feeding on lichens of the genus *Lecanora* (Fig. 1*a–d*).

The investigation was carried out at the Biological Field Station of the Imperial College of Science and Technology, Slough, Buckinghamshire, under the direction of Prof. J. W. Munro. I wish to thank Dr O. W. Richards, lecturer in entomology at the Imperial College, for suggesting the work, and for his invaluable assistance and great interest throughout.

2. HABITAT

(a) *Local distribution*

(1) *Lichen.*

Luffia ferchaultella is only found in situations having a sufficient supply of its lichen food, in particular *Lecanora*. This lichen contains the green alga *Pleurococcus*. This alga is very widespread and occurs on most tree trunks, fences, and walls in the country. It is not very common in town areas.

There are two types of green growth commonly present on tree trunks. There is a bright green form, usually damp-looking, which is composed of *Pleurococcus* only; besides this there is a darker green variety which looks drier than the previous type. This is a lichen since it is a mixture of green alga and fungal hyphae. It is certainly a *Lecanora*, probably *L. varia*, which is the commonest species of the genus. Identification of the lichen requires the reproductive bodies of the fungus. Various stages of the colonization of the *Pleurococcus* by the fungus are often present on the tree, the two forms, lichen and alga, merging into one another. *Lecanora varia* is a very primitive form of lichen, often hardly reaching the condition of a true lichen.

The moth larvae eat the *Pleurococcus* growth to some extent; but where, as often happens, both this and the lichen are on the same tree, the number of larvae present seems to be dependent on the area covered by the lichen (see Tables 1–3).

On a series of 6 in. squares on some horse chestnuts at Slough the following numbers of larvae were found.

Table 1

	Squares with *Lecanora* present	Squares with both types present	Squares with *Pleurococcus* present
Total no. of larvae in six squares	21	2	0
Average no. per square	3·5	0·3	0

A continuous belt 6 in. wide at varying heights round a similar horse chestnut was divided into types and the larvae counted:

Table 2

	Lecanora present	Both types present	*Pleurococcus* present	Height of belt (ft.)
No. of larvae	6	2	0	5
,,	9	3	0	4
,,	7	2	0	3

A more detailed count of larvae on the two types of green growth is tabulated in Table 3. It is based on a 6 in. wide area round a horse chestnut at a height of 4 ft. 6 in. above ground-level.

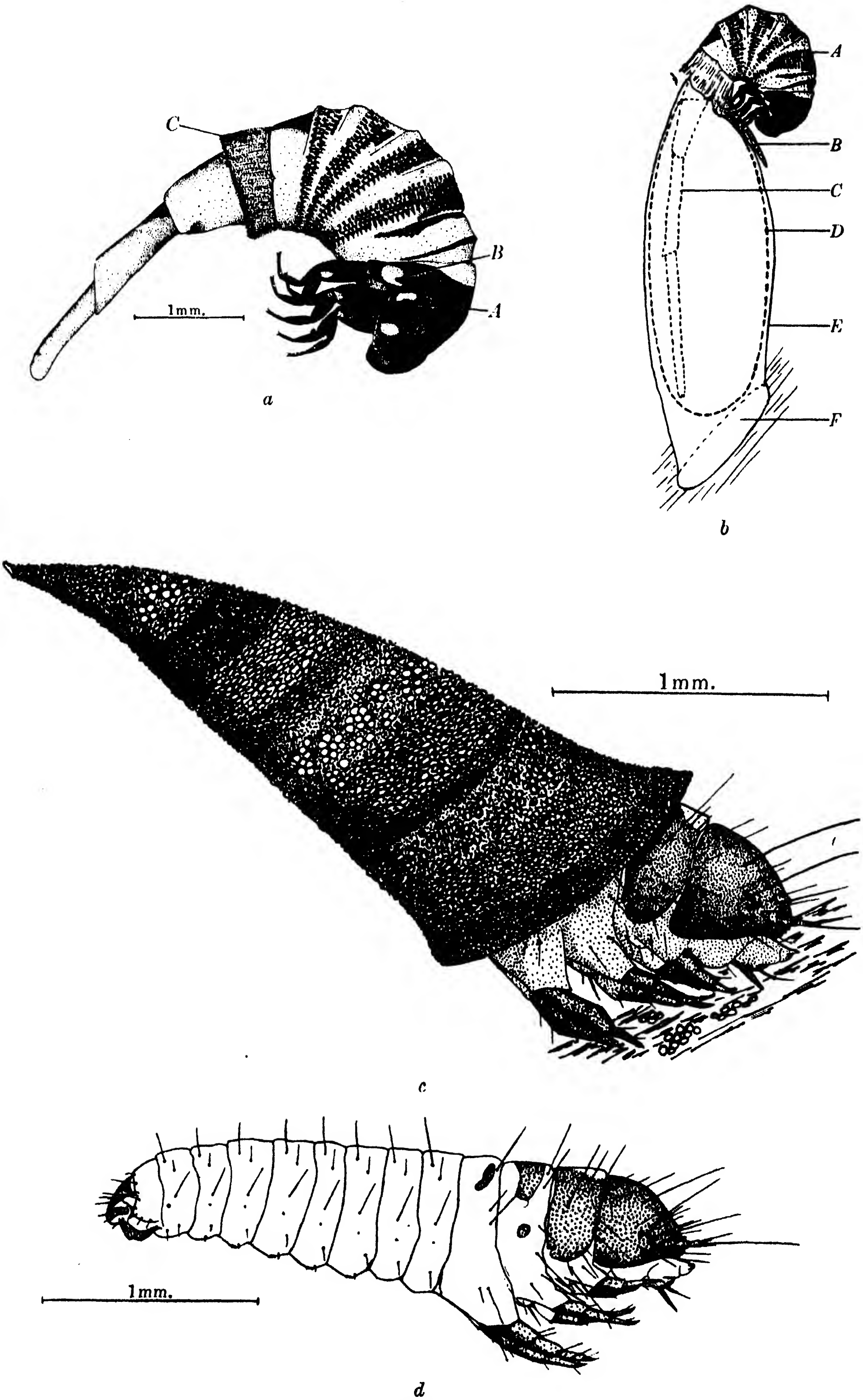


Fig. 1.

Table 3

	Length of band in.	No. of larvae Nov.	No. of larvae April	Total larvae	No. per in.
60% *Lecanora* thick growth	5	11	14	25	2·5
80% *Lecanora* patchy growth	2·5	5	6	11	2·2
90% *Lecanora* thick growth	5	28	25	53	5·3
No *Lecanora*	3	1	2	3	0·5
No *Pleurococcus*	1·5	2	1	3	1·0
80% *Pleurococcus* thick growth	6	1	0	1	0·08
Both types present but scattered	6	2	4	6	0·5
Both types present thick	6	3	4	7	0·6

It will be seen that the 12·5 in. of the band which had more than 60% *Lecanora* had the majority of the larvae. Eighty-nine larvae were on this *Lecanora*, six on the bare areas, thirteen on the mixed areas, and one on the *Pleurococcus*. The lengths of these areas were 12·5, 4·5, 12 and 6 in. respectively: the average number of larvae per inch of circumference being 7·12, 1·33, 0·5 and 0·15.

(2) *Species of tree.*

The species of tree appears to have little influence, provided the lichen is present. Trees with a deeply creviced bark tend to support a larger number of larvae than do those with a smooth bark. There are one or two exceptions to this generalization. Horse chestnuts, which usually have a smooth bark, are often well stocked with larvae. This is probably due to the heavy growth of lichen (usually *Lecanora varia*) which these trees often possess. Furthermore, the tree occurs commonly in the type of country favoured by *Luffia*, i.e. open park land type. Elms are very rarely well stocked with the moth, though they possess deeply creviced bark. This is probably due to the predominance of *Pleurococcus* only on them where a green growth occurs, though elm bark is not commonly covered by any green growth at all. A hard white lichen is very common on elms, but this does not appear to suit *Luffia ferchaultella* and *Lecanora* is rare. When the moth occurs on stones it apparently feeds on lichens other than *Lecanora varia*, though probably of the same or closely allied genus.

A census of trees near Slough likely to have the moth on their trunk (i.e. in open country) was done. The figures given in Table 4 represent approximate percentages of the different species having the larvae present in four degrees of abundance, estimated by general impressions.

Legend to Fig. 1 a–d.

Fig. 1*a*. Adult. *A*, forewing (reduced to small thoracic flap). *B*, hind wing. *C*, fringe of long scales forming an anal tuft (used by the adult to block the upper aperture of the case after oviposition in the pupa case).

Fig. 1*b*. Diagram showing oviposition. *A*, adult female. *B*, facemask of pupa case (displaced by adult on emergence). *C*, ovipositor inside pupa case. *D*, position of pupa case. *E*, algae or bark-covered larval case. *F*, spun-down mouth of larval case (larva turns round, faces the apex of the case before pupating).

Fig. 1*c*. Almost full grown larva as it appears on the tree.

Fig. 1*d*. Almost full grown larva without case.

Table 4. *Percentage of trees with larvae present in different densities*

Species	No. of trees examined	Abundance of larvae (%) None	Few	Fair no.	Numerous
Willows (*Salix*)	34	10	40	47	3
Oak (*Quercus*)	238	15	20	61	12
Horse chestnut (*Aesculus hippocastanum*)	105	25	13	26	12
Beech (*Fagus sylvatica*)	38	39	17	26	8
Elm (*Ulmus*)	175	50	28	22	0
Birch (*Betula*)	26	54	27	19	0

Willows are the most likely to have some larvae on them. The low number of willows having large numbers of larvae on them is probably due to these not usually possessing thick growths of *Lecanora*. The second best tree is oak, which has been used in this investigation to map the distribution of the moth. It is the tree most likely to be present in all localities, and to have the larvae, if the moth occurs in that place. Probably the commonest tree in this country is elm, but it is of little value for estimating the distribution of *Luffia* since a large proportion are without larvae. Though their bark is not very creviced, both beech and horse chestnut are often well inhabited, since many of them have very heavy growths of lichen, particularly when they are growing in the type of situation favoured by *Luffia ferchaultella*. Birch has the larvae on its bark when the smooth white areas have become broken. On old birch trees fairly large (though seldom *very* large) colonies of the moth have been found.

Some other trees have been observed with the moth on them. Ash (*Fraxinus elatior*) is often heavily infected. It is comparable to the oak in this respect, but it is a much less common tree and was therefore of less value in this survey. Lime (*Tilia*), apple (*Pyrus*) and plum trees (*Prunus*) are often well stocked with the moth, but the prevalence of the lime in urban areas, where lichens do not thrive, causes *Luffia* to be less common on them than on similar trees in rural districts. The same applies to planes (*Platanus acerifolia*) and sycamores (*Acer pseudoplatanus*). The moth has also been found on hornbeam (*Carpinus betulus*), rowan (*Pyrus aucuparia*), lilac (*Syringa*), locust (*Robinia pseudoacacia*), sweet chestnut (*Castania sativa*), alder (*Alnus glutinosa*), hawthorn (*Crataegus*), holly (*Ilex aquifolium*), *Laburnum*, black poplar (*Populus nigra*), Lombardy poplar (*P. italica*) and white poplar (*P. alba*). As a rule gymnosperms do not have enough lichen on them to support the moth. A few larvae have been found on silver fir (*Abies alba*), but no pupated cases were seen. Austrian pine (*Pinus nigra austriaca*), cedar (*Cedrus libanotica*), Scots pine (*Pinus sylvestris*) and yew (*Taxus baccata*) have not yielded more than a few larvae, though numerous trees have been examined.

(3) *Position of tree.*

The position of the tree is an important factor. The larvae are not found on trees in a wood if the tree is more than 20 yards from the edge, unless the

undergrowth is very thin. Trees surrounded by thick bushes do not have the moth on them. This effect is well illustrated by a group of trees studied at Epping. The result of the shading bushes is indicated in Fig. 2.

Besides this screening effect due to trees and undergrowth there is another caused by sudden rises in the ground-level. A group of trees situated on the top of a hill will more often than not be uninfested by the moth, though the trees are apparently suitable. This phenomenon has been observed in several localities, notably near Chingford in Essex, at Harrow, and also near Barnet. Small but abrupt hills have a similar effect to that caused by large hill masses, e.g. on the Chilterns (see p. 20), though the reasons for this are probably different. Gentle undulations do not affect the distribution. The optimum type of country for the moth is open park land such as Richmond Park or Windsor Great Park, where there are plenty of trees situated in unscreened positions.

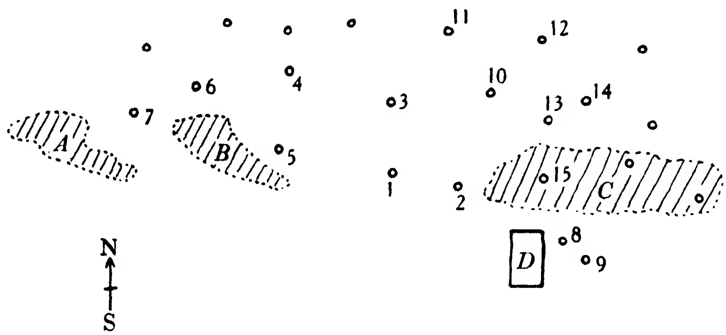


Fig. 2. Diagram map of a group of trees near Chingford. The circles represent the positions of the trees in a small area of Epping Forest near Chingford. The shaded areas *A*, *B* and *C* are groups of undergrowth, chiefly thick hawthorn. The space south of the trees is open country for over a mile. *D* is a large store hut. The only trees with an open prospect to the S.W. are 1 and 2. They alone have large numbers of moth larvae on them. 3 and 10 which are about 15 yards in from the edge of the forest have some larvae on them but not many. 4–7 and 11–15, though all well covered with *Lecanora*, are without larvae. 8 and 9 are also shaded and also lack the moth, but had very little alga on their trunks. This suggests that trees having a fairly open prospect, especially to the S.W., the weather side, tend to have more larvae on them than do trees which are protected from the wind.

(4) *Age of tree and its isolation.*

It has been found that a tree is unlikely to be inhabited by the moth before it has attained a circumference of 6–8 in. A permanent colony is not usually formed until the bark begins to be creviced. It is probable that the larvae can be carried on to trees from distances of over 1½ miles (p. 24).

(*b*) *Distribution of larvae and pupae on the tree*

Except during periodical migration the larvae tend to be more numerous on the lower parts of the trees. There is a south and east orientation, probably due to a light factor, though the prevailing west winds may have some effect.

The density of the larvae per 6 in. square on horse chestnuts at Slough is given in Table 5. The figures for each height are based on counts of about 15 squares from areas covered by *Lecanora*.

Table 5

Height above ground	Average number of larvae per square				
	North	East	South	West	Average for whole circumference
5 ft.	0·5	1·75	3·0	0·75	1·5
4 ft.	1·5	2·0	5·0	0·5	2·25
2 ft.	0·75	2·5	7·5	0·75	3·0
6 in.	3·75	3·75	19·75	3·0	6·25

The averages are given to the nearest 0·25. The counts were made in May.

The final positions of the larvae are indicated by the counts of the spun-down pupated cases made on an apple and a plum at Slough (Table 6).

Table 6

Height in ft. ...	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8
			Plum					
No. of pupae	44	84	110	60	36	20	—	—
Pupae per 6 in. sq.	0·5	0·9	1·3	0·7	0·5	0·3	—	—
			Apple					
No. of pupae	69	72	84	36	22	8	14	5
Pupae per 6 in. sq.	0·7	0·8	1·0	0·4	0·3	0·1	0·1	0·04

While the maximum number of larvae appears to be usually very near to the ground, the pupae tend to be higher up the tree. Irregular distribution is commoner on smooth bark than on well-creviced trees. The amount of alga and lichen controls the distribution of the larvae, but the pupae tend to be more affected by the distribution of cracks in the bark which act as places for pupation. There seems to be a tendency for the south and east sides of a tree to have the majority of the pupae (Table 7).

Table 7

Height on tree (ft.)		Number of pupae per quadrant				
		North	East	South	West	Total no.
0–3		11	32	27	9	79
3–5		12	14	14	2	42
0–5	Total	23	46	41	11	

(*c*) *Effect of light intensity*

A series of experiments was carried out to discover the light limit below which the larvae would not live. That such a limit existed was suggested by the distribution of the larvae on the lower and better illuminated parts of the

trunk. The intensity of illumination was measured by decomposition of oxalic acid solution by light under the catalytic action of uranyl sulphate exposed in Monax test-tubes (Atkins & Poole, 1929). The method adopted measured the mean horizontal illumination over the period when the tubes were exposed. The light values for any position were obtained in terms of a fraction of the total light present in the open during the time of measurement. The tubes were exposed for periods of 2 hr. at midday between 12 noon and 2 p.m. during May, June and July. This was the period when the larvae were most active and the trees were in leaf. Control tubes were exposed in the open, and two or three were also kept in the dark to act as zero controls.

A set of green screens was made to cover part of a tree trunk, so that the light intensity over that part of the surface was reduced. They were in three degrees of density and are referred to here as light, mid- and dark green screens. At the beginning of each experiment a known number of active larvae was placed under each of the screens. After 24 hr. the position of the larvae under the screens was noted. Two areas 4 and 6 in. square were marked under the centre of each screen. The number of larvae found in the squares was taken as a measure of the effect of the screens on the movement of the larvae compared with the movement of a similar set of larvae in a control area without the screens. The total of five such experiments using about 20 larvae each per screen is shown in Table 8.

Table 8

Screen type	No. larvae started	No. larvae found	No. found in 4 in. sq.	No. found in 6 in. sq.
Control	100	56	15	33
Dark green	104	86	6	34
Mid-green	99	63	17	37
Light green	112	85	31	55

Table 9 shows the figures expressed as percentages of the numbers found after each experiment.

Table 9

Light intensity (full light in open = 1·0)	Screen type	% in 4 in. sq.	% in 6 in. sq.
0·117	Control	26·8	56·2
0·023	Dark green	7·4	37·2
0·047	Mid-green	31·8	56·2
0·070	Light green	37·8	60·4

The number of larvae present on a tree becomes very small at a height of about 8 ft. (These results were obtained on a series of chestnuts at Slough: the figures obtained may not necessarily hold at other localities.) At the highest point at which larvae are found the light intensity was about 0·025 of that in the open. This amount of illumination was found at various heights on the trees studied at Slough; but usually it was about 7–8 ft. up the trunk and nearly always coincided with the usual upper limit of the larvae. Larvae were

found higher but only in small numbers compared with the number present on the lower portions of the trunk. It will be noted from Table 9 that the dark green screen was much more effective than the other two in causing the larvae to leave the squares under them, and that it was this one which cut down the light below the normal intensity limit of the larvae as measured on the trees. It is therefore very probable that the moth larvae will not as a rule live in nor move into areas of the tree where the light intensity is less than 0·025 of the light in the open.

The light intensities measured at various heights on the trees are illustrated by the following example:

Height (ft.)	1·0	1·5	3·5	4·5	7·0	8·5	10·0	12·0
Intensity	0·236	0·278	0·179	0·118	0·052	0·047	0·014	0·019

The greater intensity about 1–2 ft. from the ground was noted in several experiments. It is probably due to reflection from the ground. The large numbers of pupae found in this area of the trunk may be correlated with this fact. The effect of light colour upon larval movement is referred to later in the paper.

3. Distribution in England

The records of *Luffia ferchaultella* given by Tutt (1900) are not very numerous. He mentions twelve localities: four from Sussex, three from Surrey, two from Kent, and one each from Essex, Gloucestershire and Herefordshire. A study of all the available county faunal lists added a little to these records, but the number of known localities was surprisingly small, considering the abundance of the species in the south of England. On suitable trees it is often very numerous. More than 400 specimens have been collected from one tree in a locality where it was previously unrecorded. The main distribution of the species in this country has been fairly well determined during this investigation (Fig. 3).

A suitable tree, usually an oak or chestnut with adequate growth of *Lecanora*, was examined in each locality. If larval cases of *Luffia ferchaultella* were found on it, the locality was noted on the map with a spot. If no cases were found on the trees examined, the absence of the species was assumed and the locality was marked with a cross. The negative records are not to be regarded as absolute. In most localities they are based on an examination of five to ten trees which were suitable for the larvae, and would therefore be expected to have them if the species occurred in that part of the country. It can be safely assumed that where there are negative records the species, if it was present, was so in numbers far below normal.

The moth has been found to occur over the whole of south England with the exception of Cornwall. Its western limit in the south appears to be the eastern edge of Dartmoor and Exmoor. It has not been found in Wales. The

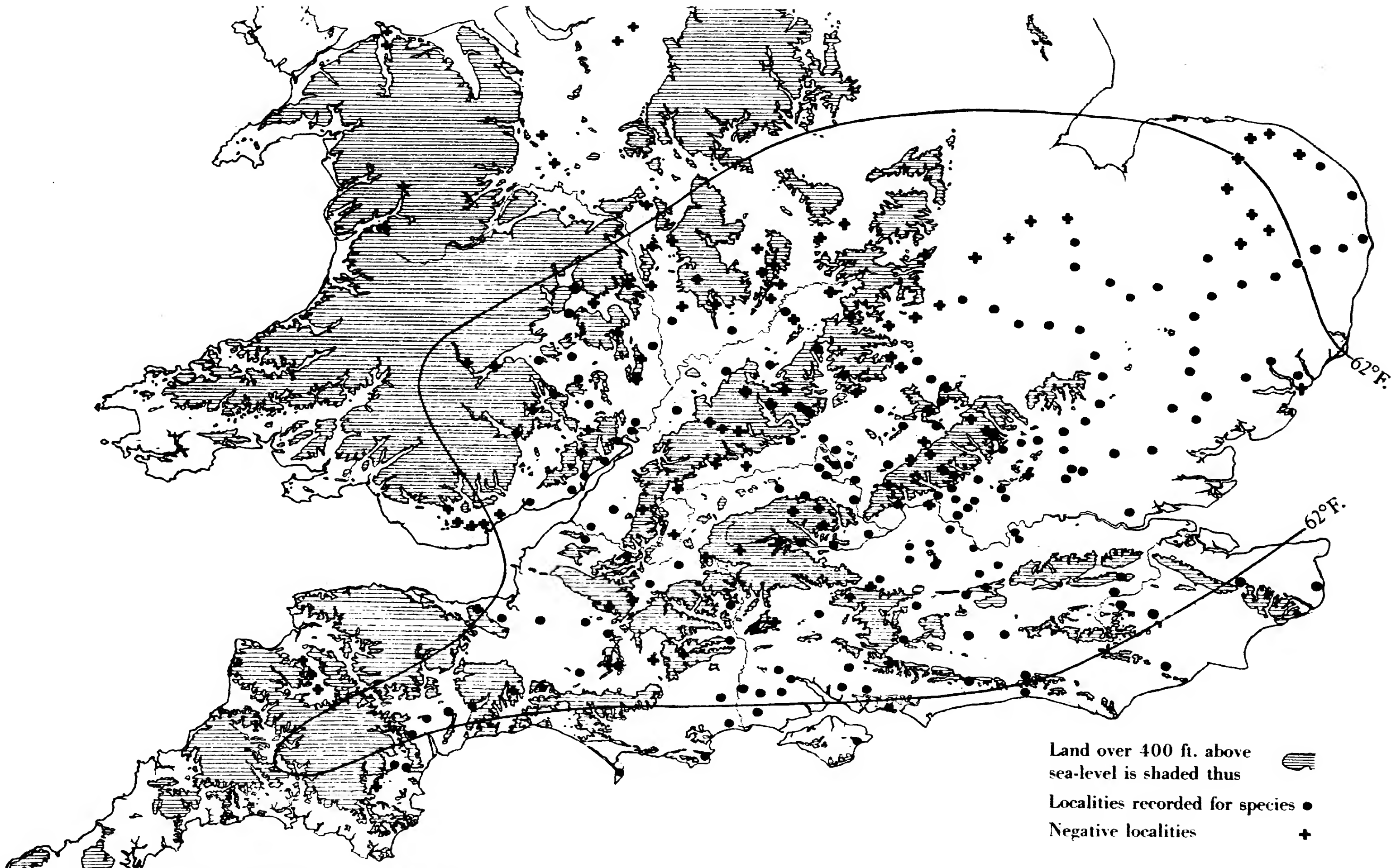


Fig. 3. Distribution of *Luffia ferchaultella* in England. Land over 400 ft. above sea-level is shaded. *Spots* mark places where the moth was found, *crosses* where it was not found. The 62° F. July isotherm is shown. The records marked are mostly the author's own, but six published by other people are also included.

western limit here seems to be near a line from Newport, Monmouth, up to Leominster. The latter is the most northerly point in the west of England where the moth has been found. It is present over the lower Severn Valley as far as Droitwich, and up the Avon to just above Warwick. The species is present over most of East Anglia. Its northerly limit appears to follow a curved course from Northampton via Kettering, March, Downham Market, Swaffham, to a few miles north of Thetford. From Thetford the limit apparently turns north and reaches the east coast near North Walsham in Norfolk.

Over this range it has been observed that the moth keeps to the valleys and is rarely found at a greater height than 400 ft. above sea-level. Both the Chiltern and Cotswold ridges produce a definite break in the distribution of the species. In the northern and eastern parts of its range it appears that the height limit becomes lower. This is particularly shown over the East Anglian Ridge and in Norfolk. It is also indicated by the distribution of the moth on the higher ground between Thames and Ouse Valleys. Near the Northampton uplands the moth becomes scarce and is absent some distance below the 400 ft. contour line. The moth is quite scarce in the Avon Valley above Warwick, and it dies out entirely below Coventry, well below the 400 ft. level. In the Severn Valley, the Clent Hills and south Shropshire Hills form a barrier to the species, which does not occur as far north as Kidderminster, though this town is much below 400 ft. above sea-level. It is present sporadically, often quite common, over the plain of Hereford, but I have found it nowhere at places over 350 ft. above sea-level.

In the upper parts of the Thames and Bristol Avon Valleys, between Lechlade and Bath, the moth seems to be very scarce, though here again the land is under 400 ft. South of the Thames it has been found over the 400 ft. line, but usually the downs have so few trees that the moth is quite uncommon. Where suitable trees occur on the higher parts the moth may be found, but it is very irregularly distributed in such places. There is an area in the New Forest district where the moth is present but uncommon. This is probably because either thick woods or open heathland occur over most of this country, and neither type of country suits the species.

The species is very common over the whole middle Thames Valley, and in the district immediately round Oxford. It is also numerous in the north of Essex. In the lower Thames area, both north and south of the river, the moth is much less common. Over the Metropolitan area it is unknown, though it occurs commonly in suitable habitats on the outskirts of Greater London.

With the exceptions noted the moth covers the rest of its range fairly evenly; in the east, where there are no hills to act as barriers the moth dies out gradually. Near the limits pupated individuals become rare, though during the early part of the moth's life-history period, late summer and autumn, large numbers of larvae can be found. These fail to survive the winter and do not pupate. A similar effect has been observed in the valleys on the south slope of

the Chilterns. As the valley ascends the number of old pupated cases gets less, though the trees examined may have numbers of early instar larvae. At the scarp slope of this ridge the density of the species increases much more rapidly. There is very little shadow effect. The same population gradient has been observed on the Cotswold Ridge.

The species covers a range nearly completely enclosed by the 62° F. (16·4° C.) isotherm for July, the month when the adults emerge and oviposit. The areas where the range overlaps the isotherm are localities with a high sunshine record for the same month. The excess hours of sunshine might be expected to make up for the slightly lower average temperature. The northern limit of the species seems to be rather far south of the 62° F. July isotherm. This could be explained by the effect of average annual temperatures on the larval stages, since apparently it is they which fail to survive the winter in the areas near the northern limit.

The records for *Luffia ferchaultella* are arranged under counties. Except for the localities marked with an asterisk, the records were obtained personally. Most of them are new county records. The moth had not been recorded previously from Bedfordshire, Cambridgeshire, Devon, Huntingdonshire, Middlesex, Monmouthshire, Norfolk, Northamptonshire, Somerset, Suffolk, Warwickshire, or Worcestershire.

The following abbreviations are used:

c. common. f.c. fairly common. v.c. very common. v.f. very few. r. rare. Names in brackets, e.g. (Tutt), after localities marked with an asterisk refer to its source.

BEDFORDSHIRE: Leighton Buzzard f.c. BERKSHIRE: Abingdon c.; Ascot f.c.; Hungerford c.; Jealotts Hill f.c.; Marpledurham c.; Newbury f.c.; Stanford in the Vale f.c.; Theale v.c.; Wallingford f.c.; Wantage f.c.; Windsor Great Park f.c.; Wokingham c.; Bagley Wood* (Microlepidoptera of Oxford District, 1928[1]); Cothill* (Microlep. Oxf. Dist. 1928); Kennington* (Microlep. Oxf. Dist. 1928); Tubney Wood* (Microlep. Oxf. Dist. 1928). BUCKINGHAMSHIRE: Amersham v.f.; Aylesbury f.c.; Beaconsfield f.c.; Bourne End f.c.; Burnham Beeches c.; Fenny Stratford f.c.; Iver c.; Langley c.; Slough c.; Rickmansworth f.c.; Waddesdon f.c.; Winter Hill (Marlow) not c.; Wolverton f.c. CAMBRIDGESHIRE: Cambridge f.c.; Caxton Gibbet not c.; Chatteris c.; Ely f.c.; Fordham not c.; March not c.; Stump Cross f.c. DEVONSHIRE: Alphington f.c.; Clyst Honiton c.; Chudleigh not c.; Honiton f.c.; Kingsteighton c. DORSETSHIRE: Sherborne f.c.; Portland* (Tutt); Purbeck* (Tutt). ESSEX: Chelmsford v.c.; Chigwell v.c.; Colchester v.c.; Earls Colne v.c.; Epping c.; Orsett not c.; Ongar c.; Stansted few; Waltham Abbey f.c.; Wendon f.c.; Witham v.c.; Bowers-Gifford* (Tutt). GLOUCESTERSHIRE: Chaxhill c.; Cheltenham f.c.; Gloucester c.; Iron Acton; Lydney c.; Newnham

[1] **Waters, E. G. R. (1929).** "A list of the micro-lepidoptera of the Oxford district." Rep. Ashmol. Nat. Hist. Soc. 1928: 1–72.

c.; Bristol* (Tutt). Hampshire: Cadnam f.c.; Cosham not c.; Frimley f.c.; Greatham not c.; Iford few; Ibsley f.c.; Lyndhurst not c.; Picket Post f.c.; Ringwood f.c.; Sleaford c.; Shedfield f.c.; Sutton Scotney f.c.; Titchfield f.c.; Totton f.c.; Wilverleyn Post f.c.; Yateley f.c. Herefordshire: Hereford f.c.; Leominster f.c.; Portway f.c.; Ross-on-Wye f.c.; Tarrington* (Tutt). Hertfordshire: Barnet f.c.; Bishop's Stortford f.c.; Hatfield c.; Leverstock Green f.c.; Redbourn c.; St Albans f.c.; Ware f.c.; Cheshunt* (Tutt). Huntingdonshire: Great Staughton f.c.; St Neots c. Kent: Sevenoaks c.; Tonbridge f.c.; Tunbridge Wells c.; Deal* (Tutt); Goudhurst* f.c. (O. W. Richards); Lewisham* (Tutt); Maidstone f.c. Middlesex: Harrow c.; Hatch End f.c.; Laleham v.c.; Northolt f.c.; Uxbridge f.c. Monmouthshire: Chepstow f.c.; Llanwepn f.c.; Magor f.c. Norfolk: Caister r.; Great Ormesby f.c.; Harleston c.; Scole f.c.; Stalham f.c.; Thetford c. Northamptonshire: Higham Ferrers not v.c. Oxfordshire: Dorchester f.c.; Henley-on-Thames f.c.; Sandford f.c.; Tetsworth f.c.; Witney r.; Woodstock r.; Dorchester*, Oxford* and Yarnton* (Microlep. Oxf. Dist. 1928). Somersetshire: Butleigh f.c.; Castle Cary not c.; Corston nr. Bath f.c.; Crewkerne f.c.; Long Ashton c.; Nether Stowey f.c.; Weston f.c.; Woolverton f.c. Suffolk: Beccles not v.c.; Bungay f.c.; Bury St Edmund's not c.; Capel c.; Hepworth few; Ipswich f.c.; Ixworth not c.; Long Melton c.; Mildenhall f.c.; Oulton not c.; Sudbury c.; Trimley c.; Wortham c. Surrey: Chertsey f.c.; Dorking not v.c.; Egham c.; Guildford not c.; Oxshott f.c.; Richmond c.; Ripley f.c.; Wimbledon c.; Camberwell* (Tutt); Claremont Park* (Tutt); Peckham (Tutt). Sussex: Battle f.c.; Horsham c.; Petworth c.; Steyning c.; Arundel* (Tutt); Hayling* (Tutt); Horsham* (Tutt); Shoreham* (Tutt). Warwickshire: Alcester f.c.; Shipston-on-Stour not c.; Warwick not c. Wiltshire: Seend f.c.; Stonehenge c. (on stones); Stonehenge* (Tutt as *L. lapidella*); Wilton f.c. Worcestershire: Droitwich f.c.; Powick c.; Wickhamford f.c.

4. Dispersal

(*a*) *From tree to tree*

(1) *Method of dispersal.*

The occurrence of the moth suggests that it is distributed by wind dispersal. Trees which were screened from the wind did not have the moth on them. During the early instars the larvae are easily blown off their trees, especially as they spin long lengths of silk which might act as parachutes (see Tutt, 1900, p. 249) in much the same manner as do the similar structures spun by some young spiders. The older larvae are less easy to blow off, but even they have been observed to be carried away when walking about on windy days. (Jones & Parks (1928) state that the first stage larvae of *Thyridopteryx ephemeraeformis* spin themselves silk parachutes and are by this means carried from one tree to another. This occurs both before and after their bags have been spun. Haseman

(1912) records the infestation of rose-bushes by wind transportation of young larvae over a distance of $\frac{1}{4}$ mile.)

Definite proof that the larvae are blown off their tree by the wind has been obtained. A number of narrow sheets of plywood, covered on one side with a thin layer of adhesive material, were set up round a tree on a cylindrical framework. There were nine boards which were 6 in. wide and 2 ft. 6 in. long arranged equidistant from each other and at a distance of 18 in. from the tree. There was about 12 in. space between each board. The tree was therefore covered for one-third of its circumference, and shielded from the wind to this extent. If any larvae were blown off there would also only be one-third of them caught on the boards. The arrangement covered effectively about 2 vertical feet of the tree at a height of 4 ft. above the ground.

Between 10 November and 10 December two larvae were caught on the boards, having presumably been blown off the tree. Since the adhesive surface was facing the tree they are very likely to have come from the tree. The tree trunk carries larvae for about the first 6 ft. It may be assumed therefore that during this month about 20 larvae may have been blown off the tree. The reverse experiment, of having adhesive surface facing outwards from the tree to catch larvae blown on to it has not been tried.

Both the larvae caught from the tree were third-instar larvae. An old pupated case was also detached and blown on to the boards. Whether older larvae can be easily blown off cannot be decided; the pupated case in question was much less heavy than an old larva would be.

(2) *Rate of colonization.*

A series of dated trees at Burnham Beeches has been used to estimate the speed with which a tree could be infected. All the trees were beeches which are smooth-barked and consequently not the ideal type of tree for the larvae to stay on. One tree planted 3 years previously (in 1932) and about 6 in. in circumference had no larvae. A 4-year-old tree (planted 1931) of the same size had at least one larva. A tree which had been there for 5 years (i.e. since 1930) had a few *Luffia* present, but it was rather less infected with lichen than were the other trees examined. A tree which had been there for 7 years (since 1928) had about 15 larvae on it, the girth of this tree being 15 in. Two older trees, 10 and 16 years old and 17 and 36 in. in circumference respectively, were well infected with the moth. All the trees studied had adequate amounts of the lichen *Lecanora*, and were all more or less well situated, and within 100 yards of each other. The oldest tree, 52 years old and 60 in. in circumference, had few larvae, possibly because of its low branches and very thick foliage—probably a light effect rather than an example of wind screening. The other trees had very few leaves. These results appear to suggest that the moth can reach a tree within 4 years of planting as a sapling. This limit is much too early if the plant is grown from a seedling. In this event the tree is unlikely to be colonized

before it has attained a circumference of 6–8 in. The youngest tree with previous year's cases on it was a 7-year-old specimen having a girth of 15 in. This is about the size at which the bark begins to be creviced.

The same set of trees was examined again in the following year. The 3-year-old tree (now 4 years) which had no larvae on it the previous year now had at least two. The 4-year (1931) tree still had only one larva. The 5-year (1930) tree that had not very much *Lecanora* on it and only a few larvae, now had at least 30 larvae though the amount of lichen was unchanged. A tree planted in 1929 and 15 in. in circumference had one pupal case of a previous year's larva; in 1935 it had no pupated cases.

It can be assumed that a tree may become colonized by the moth within 2 years of attaining a circumference of 6 in. A creviced bark is usually necessary for a permanent colony to develop.

(3) *Distance covered.*

The distance over which the moth can be transported has not been accurately estimated. The larvae have been found on trees isolated by over half a mile from other occupied trees. The larvae on the monoliths of Stonehenge are even farther from the nearest trees, a group of beeches about a mile away. These trees are not themselves colonized, for an intensive search on them failed to reveal a single larva. The nearest occupied tree was approximately 1½ miles away.

The distance over which the larvae can be carried is further indicated by the occurrence in the Chiltern valleys of early instar larvae on trees having no sign of pupal cases. Such temporary groups of larvae have been found up to 5 miles from the nearest known trees with permanent colonies on them.

(*b*) *Migrations on the tree*

It has been observed that massed migrations of the larvae on a tree may occur at times. Several of these migrations were noticed in 1935 before the full-fed larvae spun themselves down for pupation. During the year 1936, however, they were not repeated, at any rate to the same extent. Migration may be only obvious in years when the species is very numerous, as happened in 1935 when the phenomenon was noticed. The larvae moved up the tree in a more or less compact group about a month before pupation. This was noted on four trees at the Slough Biological Field Station, two trees in particular showing it very well. The subsequent behaviour of the larvae on these two trees was observed regularly. The migration which occurred during the summer 1935 is shown by the larval counts given below.

The figures italicized are the higher values noted during each count. Between 24 and 28 May the larvae moved about 3 ft. up the tree and tended to become confined to a narrower band than before. As the total number of

larvae was reduced they appeared to begin to spread again over a wider band. This may, however, be the result of the maxima becoming less distinct.

Table 10. *Migrations of larvae on plum tree*

Date ...	24 May	27 May	28 May	30 May	31 May	1 June	2 June	3 June
Height above ground (ft.)	Numbers of larvae							
0– 1	54	20	17	15	12	5	—	—
1– 2	92	41	28	28	28	17	—	—
2– 3	180	92	38	33	30	13	11	—
3– 4	150	100	30	27	21	10	8	—
4– 5	*580*	130	33	29	24	8	3	—
5– 6	*200*	*180*	28	29	31	12	7	—
6– 7	150	*700*	*997*	*840*	*474*	70	*53*	-
7– 8	70	90	*300*	*250*	*302*	*128*	*27*	—
8 –9	—	15	60	78	90	66	20	—
9–10	—	—	—	9	14	11	—	—
Total no.	1476	1368	1531	1338	1026	340	129	104

During the next year no such migration was detected. The total number of larvae present on the trees was considerably less than in 1935. There was a slight suggestion of an upward move on an apple tree about 3 June but the numbers involved were not large enough to be significant.

(c) *Factors affecting the activity of the larvae*

(1) *Temperature and humidity.*

The amount of movement occurring during the year appears to vary as the temperature changes. The humidity has also an effect. In one of his notes on the Psychidae, Chapman (1901) says that *Luffia ferchaultella* larvae hide in cracks during warm weather, presumably to avoid desiccation. He also (erroneously) states that they cannot walk over the lichens in dry weather. Consequently, he says, a wet winter gives them more opportunity to feed and hence to grow larger. It has been observed during this investigation that the larvae are only really active in mild damp conditions. On cold and windy days they are usually to be found in crevices on the trees. The effect of the weather on the species is mentioned by Burrows (1923), who observed periods of scarcity over a period of years which he ascribes to adverse conditions. Bruand (1853) also attributes this periodic scarcity to hard winter months.

During the winter the larvae are certainly less active than in the autumn and early summer. Between the beginning of December and the end of February they feed very little or not at all. During these months there is a corresponding period of cessation of growth. There is a decided increase in the proportion of the larvae which do not move for some time during this period (see Table 11). The movements were traced by putting a coloured pin touching the tip of each larval case and noting any change. Owing to the small size and surface texture of the larval cases, it was impracticable to mark individuals with paint.

Table 11. *Effect of temperature on the movement of larvae on a tree*

Date ...	Sept.– Oct.	Oct.	Oct.– Dec.	Dec.– Feb.	Feb.– Mar.	Mar.– Apr.	Apr.– May	May– June	June– July
Proportion not moved per period	0·002	0·08	0·24	0·42	0·21	0·20	0·17	0·09	0·04
Period in days	27	30	33	26	26	28	30	28	30
Proportion of days below 40° F. (4·4° C.)	0·00	0·00	0·18	0·49	0·50	0·11	0·00	0·00	0·00

During 12 days in the December–February period the temperature was continually below 35° F. (1·7° C.), while there were no days during the February–March period when the temperature failed to rise above this for some time in the day. This difference between the two periods explains why the amount of larval movement is so much less during December and February than in the next period, although the number of days having a temperature maximum below 40° F. is about the same.

The critical temperature for larval movement was estimated by experiments in a form of refrigeration apparatus in which the larvae were inactivated by cooling. The first series of experiments was carried out in March. These indicated that the larvae are inactive at temperatures below 39° F. (4·0° C.). It is possible that feeding does not occur to a great extent below 45° F. (7·0° C.).

Similar experiments were performed in May to ascertain if there was a difference in the critical temperature later in the life history of the species. No significant difference was observed in this temperature though the temperature at which the larvae regained *full* activity after cooling appeared to be 2–3° C. higher. Care was taken to standardize as far as possible the rate of initial cooling of the larvae as this was noted to have some effect on the recovery temperature.

(2) *Light.*

A well-marked positive phototropism was observed in the larvae. A number of larvae were placed under a circular glass cage which was illuminated from one side by a lighted slit. The positions of the larvae after being left for a period were recorded. If they had moved into the lighted quadrant they were considered positive. Those moved into the lateral quadrants were noted as neutral. Various colours of light were used and a summary of some of the experiments is given in Table 12.

It is of interest to note the greater effect recorded by the red light. This would tend to make the larvae migrate *from* areas illuminated by green light, i.e. foliage shaded areas, into parts having more reddish lighting. It has been noted that the larvae do migrate away from green lighted portions of the tree, though this is also caused by the actual intensity of illumination as well as the colour.

Table 12. *Effect of light on larval movement*

Light	Negative	Neutral no. larvae	Positive time	Not moved	Total time min.
White	8	62	572	120	51
Red	0	0	140	0	10
Blue	0	0	72	40	8
Green	10	175	617	205	73
Dark controls	181	116	131	89	32

The movements are given below in the form of average number per minute moving towards the light.

Light	Negative	Neutral	Positive	Not moved
White	0·16	1·22	11·20	2·35
Red	0·00	0·00	14·00	0·00
Blue	0·00	0·00	9·00	5·00
Green	0·14	2·40	8·49	2·81
Dark controls	5·65	3·63	4·10	2·78

(3) *Geotropism.*

The young larvae appeared to exhibit a certain amount of negative geotropism when in captivity. If a few larvae are placed in a tube a thick accumulation of silk on the cork and upper parts of the tube indicates where the larvae have been walking. The lower portions of the tube are usually clean. A similar result is obtained if the tube of larvae is kept in the dark. In their natural habitat this tendency to climb is not obvious except during the migrations noted above. Larvae collected just before pupating and placed in cages with a suitable log of wood on which to spin down also showed a tendency to climb, about a quarter of the larvae finally spinning their case to the muslin cover of the cage and often in the crevice between the top and the rim of the jar. It is not obvious why there is marked negative geotropism in the laboratory but not in nature. The counter action of the light does not sufficiently explain this fact.

5. SUMMARY

1. *Luffia ferchaultella* is a small wingless Psychid moth that lives on tree trunks, depending for food and a protective case upon lichens growing there. The species, age, position and algal-lichen flora of the tree all affect the moth population.

2. Light intensity influences the distribution of the larvae on the trees.

3. The general distribution of the species in England was mapped, mainly from collected samples. A large number of new locality records was obtained. The moth was not found on hills above 400 ft., nor outside the range of the average July isotherm of 62° F., except in places where there is an average of more than 210 hr. sunshine in July.

4. Evidence is given that the moth is dispersed from tree to tree by wind, that it can go at least several miles, and that mass migrations of larvae from

one part of a tree trunk to another occur, associated with high density of the population.

5. Activity of the larvae was investigated experimentally, and it was found that they were inactive below 40° F. (4° C.), that they were positively phototropic, with a preference for red light, and that they were negatively geotropic in the laboratory (though apparently not in nature). Humidity also effects activity.

REFERENCES

Atkins, W. R. D. & Poole, H. H. (1929). "The uranyl oxalate method of daylight photometry and its photo-electric standardization." Sci. Proc. R. Dublin Soc. 19: 321–39.

Bruand, T. (1853). "Essai monographique sur la tribu des Psychides." Mém. Soc. Émul. Doubs, Sér. 2, 3: 17–120.

Burrows, C. N. R. (1923). "Notes on the Psychides." Ent. Rec. 35: 57–62.

Chapman, T. A. (1901). "Notes on *Luffias*—with incidental remarks on the phenomenon of parthenogenesis." Ent. Rec. 13: 91–5.

Haseman, L. (1912). "The evergreen bagworm." Bull. Mont. Agric. Exp. Sta. 104: 316.

Jones, F. M. & Parks, H. B. (1928). "The bagworms of Texas." Bull. Tex. Dep. Agric. Exp. Sta. 382: 1–36.

Tutt, J. W. (1900). "British Lepidoptera", vol. 2. London.

THE COLONIZATION OF A NEW ROCKY SHORE AT PLYMOUTH

By HILARY B. MOORE

Marine Biological Station, Bermuda

1. Introduction

In the summer of 1935, during the construction of the new Tinside swimming pool at Plymouth, a beach of clean new stone was made round the outside of the pool; and this beach, together with the concrete outer surface of the wall of the swimming pool, gave an excellent opportunity for observation of the process of colonization of a rocky shore on a fairly large scale. Previous workers have studied the colonization of isolated blocks of stone or other substances, but the only record of the colonization of a complete new beach, of which I am aware, is that of Herpin (1935) on the newly made sandy beach at Cherbourg.

The beach at Tinside was kept under observation for two years, and the species present, and their size and abundance, recorded at intervals. For comparison, a study was made of a very similar stony beach nearby, which was sufficiently long-established to have attained a stable condition. A brief account of this older beach is given in the first part of this paper, and the development of the new beach in the second part.

2. The fauna and flora of the long-established beach

This beach lies below the Biological Station, and a few hundred yards only from the swimming pool. (Projected extensions of the bathing beach and terraces threaten to cover it over.) It is composed of stones, mainly limestone, up to 6 in. or a foot in diameter, the larger ones being scarce and chiefly restricted to the higher levels. The beach is walled in on either side by vertical rocks, of which the barnacle fauna has been described in another paper (Moore, 1936). At its upper end the beach enters a cave, and this fact no doubt accounts for the abnormality of the heights of the upper limits of some of the species on the beach, since the reduction in light intensity will reduce the algal growth, and this in turn will affect those animals which rely on the algae for either food or shelter. In any case, the purpose of the present survey was to show what species were abundant in the long-established beach, and not to deal in detail with their zonation.

The method used in the survey was to divide the beach transversely into 2 m. strips, and to note all the species seen in each strip. The mid-level of each strip was then determined with a dumpy level. The results obtained are

summarized in Table 1. As already stated, the beach was atypical at its upper end, so that no great significance must be attached to the upper limits given there. Further, many of the less noticeable species must have been omitted from the list, since, with a few exceptions, most of the identifications were of necessity made in the field. In this connexion I wish to express my indebtedness to all those workers at the Plymouth laboratory who helped with the survey and identifications, and in particular to Mr G. A. Steven, Mr T. G. Tutin, and Mr and Mrs D. P. Wilson. As the work was done at Plymouth, where a standard collection is kept, no special collection was retained.

Table 1. *Fauna and flora of the long-established beach (levels are in metres and refer to ordnance datum)*

Species	Lower limit	Upper limit
ALGAE		
PHAEOPHYCEAE		
Fucus serratus L.	< −3·33	−1·49
F. vesiculosus L.	−2·22	−0·78
Laminaria cloustoni Edm.	< −3·40	−3·40
L. digitata Lamour	< −3·40	−3·40
L. saccharina Lamour	< −3·40	−2·65
Ascophyllum nodosum Le Jol.	−2·75	−1·49
Ectocarpus sp.	Various levels	
RHODOPHYCEAE		
Porphyra umbilicalis Kutz var. *laciniata* J. Ag.	< −3·40	−1·81
Gigartina stellata Batt.	< −3·40	−1·63
Calliblepharis lanceolata Batt.	< −3·40	−3·40
Rhodymenia palmata Grev.	< −3·40	−3·40
Callophyllis laciniata Kutz.	−2·65	−2·65
Laurencia obtusa Lamour	−3·33	−3·33
Ceramium rubrum Ag.	−2·75	−1·63
Lomentaria articulata Lyngb.	−2·65	−2·12
Lithophyllum sp.	−2·22	−2·02
Polysiphonia sp.	−1·63	−1·49
CHLOROPHYCEAE		
Enteromorpha sp.	< −3·40	−0·78
Ulva lactuca L.	< −3·40	−1·07
Lichaena sp.	−2·12	−0·78
PORIFERA		
Grantia compressa (Fabr.)	< −3·40	−2·12
Halichondria panicea (Pallas)	< −3·40	−2·02
Sycon coronatum (Ellis & Sol.)	−2·75	−2·75
COELENTERATA		
Dynamena pumila (L.)	< −3·40	+0·17
Actinia equina L.	< −3·40	+0·17
Tealia felina (L.)	< −3·40	−3·33
Anemonia sulcata (Pennant)	−3·40	−3·40
ANNELIDA		
POLYCHAETA		
Spirorbis borealis Daudin	< −3·40	−1·04
Pomatoceros triqueter (L.)	< −3·40	−1·07
Lanice conchilega (Pallas)	−3·33	−3·33
Nereis cultrifera (Grube)	−3·40	−2·65
N. pelagica L.	< −3·40	−2·75
Lagisca extenuata (Grube)	< −3·40	−2·75
Odontosyllis ctenostoma Clap.	−3·03	−3·03
Eunice harassi Aud. & Edw.	−3·40	−3·40
Audounia tentaculata (Mont.)	−3·40	−2·65
Cirratulus cirratus (O. F. Müller)	−2·65	−1·04

Table 1 (*continued*)

Species	Lower limit	Upper limit
PLATYHELMINTHES		
Fecampia erythrocephala A. Giard	−1·04	−1·00
ECHINODERMATA		
Amphipholis squamata (Della Chiaje)	−3·03	−2·65
CRUSTACEA		
Ligia oceanica (L.)	−2·22	+2·07 >
Idotea baltica (Pallas)	−1·81	−1·81
Jaera marina (Fabr.)	−2·75	1·04
Gammarus marinus Leach	−2·22	−1·04
G. locusta (L.)	3·40	2·02
Talitrus saltator (Mont.)	+0·98	+2·07 >
Melita palmata (Mont.)	−3·40	−1·07
Apherusa jurinei (H. M.-Edw.)	−2·75	1·20
Balanus balanoides (L.)	−3·40	−0·78
B. crenatus Brug.	< −3·40	−2·43
B. perforatus Brug.	−3·40	−2·12
Verruca stroemia (O. F. Müller)	−3·40	−2·12
Porcellana platycheles (Penn.)	< −3·40	−3·40
P. longicornis (L.)	< −3·40	−3·40
Eupagurus bernhardus (L.)	−3·40	3·40
Cancer pagurus L.	−3·40	2·75
Carcinus maenas (Penn.)	< −3·40	+0·39
INSECTA		
Lipura maritima Guérin	−1·04	−0·15
MOLLUSCA		
Gibbula umbilicalis (da Costa)	−3·40	−2·02
G. cineraria (L.)	< −3·40	−1·81
Littorina littorea (L.)	−3·33	−1·00
L. rudis (Maton)	−2·75	+0·39
L. obtusata (L.)	−2·43	1·04
L. neritoides (L.)	−1·27	1·27
Patella vulgata L.	< −3·40	−1·04
Purpura lapillus L.	−3·40	−2·02
Nassarius reticulatus (L.)	< 3·40	−3·40
Trivia monacha (da Costa)	< 3·40	−3·40
Cingula cingillus (Mont.)	−2·12	+0·98
Leucopepla bidentata (Mont.)	−1·49	+0·17
Phytia myosotis (Draparnaud)	+0·39	+2·07
Lamellaria perspicua (L.)	−3·40	−3·33
Goniodoris nodosa (Mont.)	−3·40	−3·40
Heteranomia squamula (L.)	< −3·40	−2·12
Mytilus edulis L.	−3·40	1·63
Tapes sp. (juv.)	−2·65	−2·65
POLYZOA		
Membranipora sp.	−3·33	−1·20
TUNICATA		
Trididemnum tenerum Verrill	< 3·40	−3·40
Botryllus schlosseri (Pallas)	< −3·40	−2·75
Dendrodoa grossularia (van Beneden)	−2·22	−2·22

As will be seen from the list, the fauna and flora are quite typical of a beach subject to a certain amount of estuarine influence. The sessile species had, in general, not grown to so large a size on the small stones as on the bigger rocks, since the former are liable to be overturned both by people collecting, and by winter storms. However it was clear that there were ample larvae available to colonize any suitable habitat. The occurrence of the two pulmonate molluscs,

Phytia myosotis and *Leucopepla bidentata*, is worthy of note. Both were abundant, together with *Cingula cingillus*, in the upper levels of the shore, but their distribution seemed to vary from time to time, and when the survey was made they were not recorded from levels nearly as high as those at which they had been found on previous occasions.

3. Fauna and flora of the new beach

The stone from which the new beach was made is limestone, and was blasted from the position now occupied by the swimming pool, so that it may be considered as sterile when laid down. The outer face of the pool is concrete, and was completed about the end of May, 1935. The tipping of stone on to the beach was completed by the end of August of the same year. There was a certain amount of shifting of the stones on the beach by wave action, particularly during the first winter; and also, towards the end of the period of observation, by boys looking for crabs. No exact details of level have therefore been attempted, but most of the new beach lies between low water of ordinary neap tides and mid-tide level, while the pool wall rises well above high water.

At first there was no fine material among the stones of the beach, but by August 1937 a definite muddy gravel was beginning to accumulate under the stones, together with its typical fauna of polychaetes, etc. The beach below the Biological Station faces roughly south, while the new one faces east to south-east and is slightly sheltered to the south by a reef; but the difference in wave exposure of the two beaches is probably not great. Detailed notes on the several species are given below, the general progress of colonization being discussed later. The beach was examined on the following dates: 9 and 15 November 1935; 8 February, 23 April, 21 August, and 2 November 1936; 1 March and 23 August 1937.

Fucus serratus.[1] First appeared in March 1937 on the stones on the shore, where plants up to 10 cm. long were found. Unless some of the small unidentified *Fucus* seen on the stones the previous November were this species, they must have grown there since that date. In August 1937 conditions on the stones were similar, *F. serratus* still being scarce, but on the part of the wall kept damp by an outfall from the pool, plants of *F. serratus* up to 30 cm. high were fairly common. These must have grown there since March, because none were seen then.

Fucus vesiculosus. With the exception of a small plant of *Fucus* (sp.?) on the wall of the swimming pool in November 1935, no fucoids of any sort were seen until November 1936. By then a few plants of *F. vesiculosus* up to 25 cm. long were growing on the walls, and a few small plants (sp.?) on some of the rocks. As none were seen on the wall in August 1936, this considerable growth must have taken place within about two and a half months. In March 1937 conditions showed little change, but by August the plants on the wall were more abundant, and some had attained a length of 30 cm.; and some too were fruiting. On the rocks there were still only a few small plants.

[1] Species authorities are only inserted in the text for species not in Table 1.

Fucus spiralis L. var. *platycarpus* Thur. A lot of small plants, 2–5 cm. long, were found on the wall in March 1937. They were not recorded from there the previous November, nor were any seen in August 1937, so they would appear to have been a temporary colonization which did not survive.

Pelvetia canaliculata Dcne. et Thur. One or two small plants about 3 cm. high, which were seen on the wall in March 1937, but not either the previous November or the following August.

Himanthalea lorea Lyngb. Some small buttons of this species were found under stones near low water in November 1936, but not recorded subsequently.

Laminaria digitata. A few small plants about 10 cm. long were found on rocks at low water in March 1937. These might possibly have been washed in on stones from deeper water during the winter. They were not noticed the previous November.

Porphyra umbilicalis var. *laciniata*. One of the first colonizers of both wall and rocks. In November 1935 it was present on both, though smaller on the rocks than on the wall. In February 1936 plants up to 10 cm. long were common on the wall, and conditions were very similar in April and August. The plants became very dry during the summer, and are noted as much reduced in numbers in November 1936. In March 1937 they were again abundant and generally distributed on both rocks and wall; but in August they again showed the effect of desiccation on the wall, while remaining abundant and well grown on the rocks, where the lower tidal level, and greater shelter from the sun, resulted in less desiccation. Knight & Parke (1931, p. 77) note that this alga "can withstand considerable exposure but is frequently destroyed in summer when calm sunny weather prevails".

Rhodymenia palmata. Fairly common, and up to a length of 15 cm., on rocks at low water, in August 1937, but not seen there the previous March.

Bangia fuscopurpurea Lyngb. Identified as forming a considerable part of the felt on the wall in November 1935, and, although not specifically identified thereafter, was probably present.

Enteromorpha sp. Probably both *E. compressa* (L.) and *E. intestinalis* (L.) were present. *Enteromorpha* was found on both wall and rocks at the earliest examination in November 1935, and young plants comprised much of the algal felt covering the wall. In February 1936, plants on the wall were recorded up to 30 cm. long, and at all subsequent examinations they were abundant on both rocks and wall, and particularly well grown on the latter in the damp region near the outfall.

Ulva lactuca. Scattered, but common, on both wall and rocks from the first examination in November 1935. Became rather more abundant the following year, and is noted as becoming very dry on the wall in summer.

Grantia compressa. A few small ones seen under rocks in November 1936 but not subsequently.

Halichondria panicea. A single colony, 4 cm. in diameter, was found under a rock in April 1936, and good-sized masses were present in small numbers under rocks in August 1937.

Sycon coronatum. A few small ones found under rocks in November 1936 and some very small ones in August 1937.

Dynamena pumila. First noted as a good growth on rocks in August 1936, but may have been present before this. Remained common thereafter.

Actinia equina. The only sea-anemone found in the area at any time was a small specimen of this species, about 5 mm. in diameter, under a stone in April 1936.

Spirorbis borealis. None was found in November 1935, but by the following February they were abundant and well grown under the rocks, and remained so throughout the observations. In August 1937 there was a heavy settlement of very small individuals, presumably 1937 spat.

Pomatoceros triqueter. In November 1935 these were fairly abundant under the rocks, and ranged in length up to 15 mm. By February 1936 they were more numerous, and ranged up to 20 mm., and by April of that year they were fully grown. Thereafter all sizes were abundant under stones.

Serpula vermicularis L. One or two found, along with *Pomatoceros*, under stones, in August 1937.

Nereis pelagica, *Harmothoe* sp., *Glycera* sp., *Polydora* sp. When a muddy gravel began to accumulate under the stones on the beach, all these worms appeared in numbers in it, or in the muddy water under the stones. They were first recorded in August 1937, and were mostly too young for positive identification. The *Polydora* in particular were particularly abundant.

Membranipora sp. First appeared on the underside of stones in November 1936, and thereafter was very abundant there.

Bowerbankia sp. Some was found under stones in August 1937.

Amphipholis squamata. Appeared very abundantly in the muddy gravel under stones near low water in August 1937, was not seen there previously.

Balanus balanoides. Spat-fall of this species of barnacle usually occurs about April–May, although a few larvae may settle later in the year. The 1935 spat-fall seems to have missed the beach except for a very few individuals which were found under stones in April 1936, at a length of about 7 mm., and one or two seen on the wall in August and November 1936 at 7 and 8 mm. respectively. The 1936 spat seems to have settled later on the rocks and wall than it did on the long-established rocks of the neighbouring reefs where it was abundant in April, although not yet present on rocks or wall. Later a certain number settled on the latter, and in August 1936 and again in March 1937 they are recorded as fairly common on the rocks, and sparsely distributed on the wall, and about 6 mm. long in the latter habitat. By August 1937 this 1936 brood was still present in small numbers on the rocks, and a few survived on the wall also. The 1937 brood had by then settled in considerable quantities, although nowhere sufficiently to produce the overcrowding found on the neighbouring reefs. The general impression gained was one of small density of settlement of larvae and rather poor survival rate on both wall and rocks, but of normal growth rate among those which did survive.

Balanus crenatus. A few, about 8 mm. long, were found under rocks near low water in August 1936, and they were common there in November. These were most probably 1936 spat. In August 1937 well-grown individuals were present there in small numbers.

Balanus perforatus. One, about 5 mm. in diameter, was found under a stone in April 1936. In November a few more were found, apparently falling into two size groups of 5 and 9 mm. means, but it is very doubtful whether this signifies two year groups. In August 1937 small individuals were still present in small numbers under stones.

Chthamalus stellatus (Poli). No 1935 spat settled, but in November 1936 a fair quantity of the 1936 spat was found on the wall, mostly settled in patches cleared by *Patella*. They averaged 2 mm. long, the largest being 4 mm. The following March they are recorded as generally distributed on the wall, but less common than *Balanus balanoides*, and the maximum size found was 5 mm. Conditions were very similar in August 1937, very few of that year's spat having settled, it being rather early in the season for them.

Verruca stroemia. Two specimens were found in November 1935 on a *Gibbula cineraria* under a stone, but this had probably migrated in from another area. Thereafter none was seen until August 1937 when young individuals were found in small numbers under stones at low water. They were probably the spat of that year, since Bassindale (1936) says that this species breeds at Plymouth some time between March–April and September.

Porcellana platycheles. A few small ones were found under stones in April 1936. Throughout

that year they were scarce, but by August 1937 all sizes were present and common under stones near low water.

Porcellana longicornis. A few were found, for the first time, under stones, in August 1937.

Galathea squamifera Leach. One was taken under a stone at low water in August 1937.

Cancer pagurus, Portunus puber (L.). A few small specimens of both these crabs were found under stones from February 1936 onward.

Carcinus maenas. Several were found under stones in November 1935, and by the following April they were quite common, and remained so throughout the observations. With this, and other active species, it is probable that much of the colonization was by well-grown animals, and not only by larvae.

Gibbula umbilicalis. A single specimen was found under a stone in November 1935, but thereafter none was seen until March 1937, when they were fairly common under stones near low water, although considerably less common than *G. cineraria.* The same was true in August.

Gibbula cineraria. This was the commonest Gastropod on the rocky part of the shore. Good-sized individuals were common throughout the period of observation, from November 1935 onward, and their abundance at that early date suggests that they must have migrated in when full grown.

Littorina rudis. Little is known of the growth rate or general biology of this Gastropod. It is viviparous, and presumably its only means of dispersal is by crawling from one place to another, except in so far as the small individuals may be carried about by wave action. In November 1935, a single specimen was seen on the wall, having presumably crawled there from outside. The following February, a few were to be found all over the wall, living in crevices, and mostly having a space of 1–3 cm. cleared from the algal felt round the crevice. In April 1936 they had attained an average height of 6 mm., and few larger than this were ever found on the wall, the largest recorded being 9 mm. From April on they were fairly common all over the wall, but none was taken on the rocks.

Littorina obtusata. One or two were found on weed growing on the rocks, and on the rocks themselves, in November 1936. In August 1937 they were present in small numbers on the rocks, but not in nearly such abundance as on the neighbouring reefs.

Littorina neritoides. These were first found in March 1937, when individuals up to 3·8 mm. high were fairly common in the upper crevices on the wall.

Patella vulgata (including var. *intermedia* and var. *depressa*). According to Lebour (1937) the principal breeding period of this limpet is in the winter, and Orton (1928) records spat of 2–8 mm. in length as being common at Plymouth in June. In November 1935 no spat were seen on the wall, although very small ones may have been present among the algal felt. In February 1936 however, they were present on the wall in considerable numbers, and at a length of 5–15 mm. One or two of the largest of these had probably migrated in from the surrounding reefs, but the rest had almost certainly settled as larvae. By April 1936, the young on the wall, presumably the 1935 brood, averaged 15 mm. long, and a few were as much as 20 mm. In August they ranged from 25 to 30 mm., and in November the largest were 37 mm. long. No young of the 1936 brood were found at that time, but in August 1937, small individuals of 5–15 mm. were common on the wall. The larger ones were then being taken by boys, so the average size could not be determined. In April 1936, a single specimen, 15 mm. long, was taken on a stone, and by August 1937, all sizes were fairly common on the rocks. The high growth rates indicated by these figures confirm Orton's results. His figures of 26–35 mm. long at one year old in 1912, and 11–27 mm. in 1913 at the same age, compared with 6–9 mm. at St Malo (Hatton, 1936), indicate much more favourable growing conditions at Plymouth.

Cingula cingillus. Full grown specimens were very numerous under stones in August 1937, but none was recorded previous to that date.

Heteranomia squamula. None was seen in November 1935, but the following February they were very abundant, at a diameter of about 5 mm., under stones. By August 1936 they had grown to about 10 mm. diameter, which seemed to be their upper limit in this locality. At all times after February 1936 they were abundant under stones.

Mytilus edulis. A few, about 5 mm. long, presumably 1936 spat, were found under stones in August 1936. In November these averaged about 10 mm., and in August 1937 they ranged from 2 to 15 mm., and were fairly common, having probably been added to by a later spat-fall. Orton's figures for Plymouth, in 1919, are 35–40 mm. long at one year old, but only 13–16 mm. at two years on a wave-exposed shore. The rate observed at Tinside lies between these values, but the shells were clean and smooth and not of the rough, stunted type usually associated with a wave-exposed shore.

Botryllus schlosseri. In November 1935, several one-star colonies were found under stones at low water. In February 1936 they were common, and one colony measuring 40 by 40 mm. was found. By August 1936, colonies up to 120 mm. in diameter were common, and thereafter this species was present under most stones near low water.

Botrylloides leachii Savigny. Colonies were found for the first time, and very abundantly, under stones, in August 1937.

4. The general process of colonization

Kitching (1937, p. 484), summarizing previous work on recolonization in the littoral zone, says: "No generalization can be made from the work described above, except that it leads to the impression that recolonization is a somewhat haphazard process, in which the sequence is determined largely by the order of arrival of pelagic larvae and spores. Little evidence has been brought forward to suggest that the establishment of one organism assists either in the establishment or in the elimination of any other." Later, summarizing his own results, this time in a sublittoral habitat, he says (p. 494): "It is concluded that those sessile organisms which finally become established eliminate their predecessors by smothering them or by occupying all the space available for anchorage. The earlier arrivals do not appear to facilitate in any way the establishment of the later ones, except in so far as they form a substratum for them. The slower growing but persistently spreading perennials eventually triumph. It is also concluded that the chief factors which influence the sequence of appearance of mature organisms upon a denuded rock area are (*a*) the time of arrival of spores or larvae of species viable under existing conditions, and (*b*) the growth rate of these species under these conditions." Hatton (1932), on the other hand, has shown that young *Fucus vesiculosus* will not survive unless kept damp either by older plants of the same species or by a felt of *Enteromorpha.*

While it is true that this same sequence of *Enteromorpha* felt followed by Fucoids was observed at Tinside, it was nearly two years after the completion of the wall that Fucoids began to be abundant, while the *Enteromorpha* felt was present almost from the first. And, as Fucoid spores must have been present almost throughout the year, it would appear that some other factor

deterrent to their establishment was operative, though what this was is not apparent. *Enteromorpha*, *Ulva* and *Porphyra*, on the other hand, seem to have found the environment congenial from the first.

Of the attached, suspension-feeding animals, *Spirorbis* and *Pomatoceros*, and the lamellibranch *Heteranomia*, settled in large numbers from the start, and to a lesser extent also, *Botryllus*. The various barnacles, with their more limited breeding seasons, did not appear until the second summer, and then not in nearly such great numbers as on the neighbouring reefs. This is of interest, since several authors speak of the great numbers of barnacle spat settling on test material newly placed in the sea. On the wall they may have found some difficulty in finding space in the thick algal felt, and this is also suggested by the fact that they were thickest in the spaces browsed clear by *Patella*, but this felt was not so thick on the rocks lower on the shore, and it looks as if new limestone rock, which has not been weathered by contact with the sea, does not form a really attractive surface for the attachment of young barnacles. Once settled, their growth appears quite normal for the locality. Finally, sponges, which are quite common on the neighbouring long-established beach, were markedly slow in appearance at Tinside, even after two years, and sea-anemones hardly appeared at all.

Of the deposit- and alga-eating forms, there is in most cases more doubt as to their origin. The *Patella*, which were fairly plentiful at an early date on the wall, must have arrived there as larvae. They seem to have come as soon as there was an algal felt for them to feed on. *Littorina rudis*, which is viviparous, and which also appeared on the wall at an early date, presumably reached the wall as a few adults migrating from another area, and those, breeding rapidly, soon colonized the available space. *Gibbula cineraria* was found fully grown so early, and in such numbers, that there must almost certainly have been a considerable migration of this species from deeper water into the rocky zone near low water. These were probably added to later by larvae settling in the area. It is curious that *G. umbilicalis* should have been so much slower in appearing, and should have remained so much rarer than *G. cineraria*. The young of both species settle in considerable numbers in the sublittoral and lower littoral zones, but the adults of *G. cineraria* usually extend considerably higher on the shore than those of *G. umbilicalis*. It might be expected therefore that the former would show a stronger tendency to migrate up the shore on to the area immediately above low water than would the latter, a similar behaviour having been demonstrated in the several species of *Littorina* occupying different zones on the shore (Gowanloch & Hayes, 1926), and if this were so it would explain the observed facts.

The general impression gained from two years' observation on the colonization of this piece of shore is definitely not one of keen competition for foothold among those species whose larvae are fortunate enough to settle before all the available space is occupied, but rather of a very gradual occupation, with

only some half dozen species capable of finding conditions suitable from the first. To the great majority of those species which were to be expected from comparison with a neighbouring old-established beach, conditions were obviously unsuitable at the commencement of observations, and for many they had not yet become suitable even after a lapse of two years. There is little clue as to what constitutes suitable conditions, but the fact that some species, although sparsely distributed as compared with neighbouring areas, yet showed a normal growth rate, suggests that the difficulty of survival occurs among the newly settled young, and not among the adults.

5. Summary

A newly made stone beach at Plymouth was kept under observation for two years and the progress of colonization noted. A long-established beach close by afforded a standard for comparison. Very few species colonized the beach in any numbers during that time, and it is suggested that the apparently unfavourable conditions affected the newly settled young more strongly than the older individuals.

REFERENCES

Bassindale, R. (1936). "The developmental stages of three English barnacles, *Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli) and *Verruca stroemia* (O. F. Müller)." Proc. Zool. Soc. Lond.: 57–74.

Gowanloch, J. N. & Hayes, F. R. (1926). "Contributions to the study of marine gastropods. I. Physical factors, behaviour and intertidal life of *Littorina*." Contr. Canad. Biol., N.S., 3: 133–65.

Hatton, H. (1932). "Quelques observations sur le peuplement en *Fucus vesiculosus* des surfaces rocheuses dénudées." Bull. Lab. Mar. Saint-Servan, 9: 1–6.

Hatton, H. (1936). "Observations sur l'habitat et sur la croissance de *Patella vulgata* L." Bull. Lab. Mar. Dinard, 15:17–20.

Herpin, R. (1935). "Le peuplement d'une place vide dans la nature (la nouvelle plage de Cherbourg)." Ann. Sci. nat. 18: 145–70.

Kitching, J. A. (1937). "Studies in sublittoral ecology. II. Recolonization at the upper margin of the sublittoral region; with a note on the denudation of *Laminaria* forest by storms." J. Ecol. 25: 482–95.

Knight, M. & Parke, M. W. (1931). "Manx Algae." Lpool Mar. Biol. Comm. Mem. No. 30: 1–155.

Lebour, M. V. (1937). "The eggs and larvae of the British Prosobranchs with special reference to those living in the plankton." J. Mar. Biol. Ass. U.K. 22: 105–66.

Moore, H. B. (1936). "The biology of *Balanus balanoides*. V. Distribution in the Plymouth area." J. Mar. Biol. Ass. U.K. 20: 701–16.

Orton, J. H. (1928). "Observations on *Patella vulgata*. Part I. Sex phenomena, breeding and shell-growth." J. Mar. Biol. Ass. U.K. 15: 851–62.

THE HABITAT DISTRIBUTION OF BRITISH WOODLAND BIRDS[1]

BY DAVID LACK AND L. S. V. VENABLES

(*With Plates* 1–3)

CONTENTS

	PAGE
1. Introduction	39
2. Acknowledgements	40
3. List of all species mentioned in the text	41
4. Definition of a woodland bird	41
5. The requirements of woodland birds	43
6. Methods of survey	46
7. Some habitat factors:	
(*a*) Birds of open as opposed to closed woods	48
(*b*) Birds dependent on secondary growth	50
(*c*) Hole-nesting birds	52
(*d*) Birds dependent on tall trees	53
(*e*) Birds dependent on water	53
8. Comparison of communities in different woodland types:	
(*a*) Broad-leaved deciduous woods, excluding birch	54
(*b*) Beech woods	56
(*c*) Birch woods	57
(*d*) Other broad-leaved woods	58
(*e*) Pine woods	58
(*f*) Larch woods	60
(*g*) Other coniferous woods	60
(*h*) Mixed broad-leaved and coniferous woods	61
9. Winter distributions	61
10. Distributions at other seasons	63
11. Comparison with the North European mainland	63
12. Historical considerations	65
13. Factors influencing habitat distribution	66
14. The woodland bird community	68
15. Summary	69
References	70
Appendix: Complete tabulated counts from surveys	71

1. INTRODUCTION

A PAPER by Elton (**2**), organized as a result of a broadcast talk in 1933, was the first attempt to classify the habitat distributions of British woodland birds, and he there suggested that a more detailed investigation would be profitable. The band of observers now organized under the British Trust for Ornithology

[1] Publication of the British Trust for Ornithology.

provided a suitable machinery for a more extensive survey applying to all British woodland birds in all the main types of wood in the main geographical regions of Britain. In the present state of knowledge, such a general survey, though necessarily less detailed, was felt to be more valuable than concentrated study on a few species or woodland types. The object of the enquiry was an analysis of habitat distributions, to investigate which factors provided by woods were important in habitat limitations, and to compare the differences in species composition of the different woodland types, as in the admirable study by Palmgren (**9**) for Finland. It should be stressed that the total individual bird populations of woods, with related problems, were not an object of the present enquiry; these are being studied by W. B. Alexander and the Oxford Bird Census. Nor were the geographical distributions of British woodland birds investigated, except where these have some bearing on habitat; this knowledge is summarized in the new *Handbook of British Birds*.

2. Acknowledgements

The writers wish to thank the following observers (members of the British Trust for Ornithology and others) for assisting in the present enquiry by taking counts in one or more woods:

H. G. Alexander, W. B. Alexander, M. Barclay, J. A. G. Barnes, Col. Benson, C. W. Benson, Bishop's Stortford School Nat. Hist. Soc., E. Blezard, R. Blockey, A. W. Boyd, E. H. Bray, R. H. Brown, M. H. Butterworth, Cambridge Bird Club, P. J. Campbell, W. D. Campbell, P. A. Clancey, G. H. Clegg, C. L. Collennette, H. A. Course, H. F. I. Elliott, J. C. S. Ellis, F. Fincher, James Fisher, A. Fowler, R. M. Garnett, E. Giles, J. D. P. Graham, R. H. Hardy, R. Harkness, P. A. D. Hollom, M. R. Jellicoe, A. R. Jenkins, K. P. Keywood, F. H. Lancum, London Nat. Hist. Soc., W. Marshall, V. Maxse, V. Maynard, Midlothian Orn. Club, J. D. Mills, A. R. G. Morrison, E. F. Neville, E. M. Nicholson, Oxford Orn. Soc., L. Parmenter, E. W. Pedler, H. M. Rait Kerr, K. B. Rooke, I. M. N. Ryan, H. N. Southern, R. J. Spittle, F. K. Staunton, J. P. Utley, H. E. Wall.

A summary of each count is given in the Appendix. On account of considerations of space, it was not possible to give full details of each individual count, but the more detailed surveys, such as Mr H. A. Course's weekly walk for a period of over a year through a beech wood, have been deposited with the British Trust for Ornithology for the benefit of future workers.

The writers also wish to thank the members of the scientific advisory committee of the British Trust for Ornithology for supplying further information, not elicited by the counts, on the habitat distribution of rarer species, and also for valuable criticisms during the progress of the work.

3. LIST OF ALL SPECIES MENTIONED IN THE TEXT

List of birds mentioned in the text or included in the tables, with the scientific names given in Witherby's Practical Handbook of British Birds (1924), vol. 2, pp. 903–36

Hooded crow (*Corvus cornix*)
Carrion crow (*Corvus corone*)
Rook (*Corvus frugilegus*)
Jackdaw (*Coloeus monedula*)
Magpie (*Pica pica*)
Jay (*Garrulus glandarius*)
Starling (*Sturnus vulgaris*)
Hawfinch (*Coccothraustes coccothraustes*)
Greenfinch (*Chloris chloris*)
Goldfinch (*Carduelis carduelis*)
Siskin (*Carduelis spinus*)
Lesser redpoll (*Carduelis linaria cabaret*)
Linnet (*Carduelis cannabina*)
Bullfinch (*Pyrrhula pyrrhula*)
Crossbill (*Loxia curvirostra*)
Chaffinch (*Fringilla coelebs*)
Brambling (*Fringilla montifringilla*)
House sparrow (*Passer domesticus*)
Tree sparrow (*Passer montanus*)
Yellow bunting (*Emberiza citrinella*)
Cirl bunting (*Emberiza cirlus*)
Woodlark (*Lullula arborea*)
Tree pipit (*Anthus trivialis*)
Meadow pipit (*Anthus pratensis*)
Grey wagtail (*Motacilla cinerea*)
Tree creeper (*Certhia familiaris*)
Nuthatch (*Sitta europoea*)
Great tit (*Parus major*)
Blue tit (*Parus coeruleus*)
Coal tit (*Parus ater*)
Crested tit (*Parus cristatus*)
Marsh tit (*Parus palustris*)
Willow tit (*Parus atricapillus*)
Long-tailed tit (*Aegithalos caudatus*)
Goldcrest (*Regulus regulus*)
Spotted flycatcher (*Muscicapa striata*)
Pied flycatcher (*Muscicapa hypoleuca*)
Chiffchaff (*Phylloscopus collybita*)
Willow warbler (*Phylloscopus trochilus*)
Wood warbler (*Phylloscopus sibilatrix*)
Garden warbler (*Sylvia borin*)
Blackcap (*Sylvia atricapilla*)
Whitethroat (*Sylvia communis*)
Lesser whitethroat (*Sylvia curruca*)
Fieldfare (*Turdus pilaris*)
Mistle thrush (*Turdus viscivorus*)
Song thrush (*Turdus philomelus*)
Redwing (*Turdus musicus*)
Ring ouzel (*Turdus torquatus*)
Blackbird (*Turdus merula*)
Redstart (*Phoenicurus phoenicurus*)
Nightingale (*Luscinia megarhyncha*)
Robin (*Erithacus rubecula*)
Dunnock or hedge sparrow (*Prunella modularis*)
Wren (*Troglodytes troglodytes*)
Nightjar (*Caprimulgus europoeus*)
Green woodpecker (*Picus viridis*)
Great spotted woodpecker (*Dryobates major*)
Lesser spotted woodpecker (*Dryobates minor*)
Wryneck (*Jynx torquilla*)
Cuckoo (*Cuculus canorus*)
Little owl (*Athene noctua*)
Long-eared owl (*Asio otus*)
Tawny owl (*Strix aluco*)
Barn owl (*Tyto alba*)
Hobby (*Falco subbuteo*)
Kestrel (*Falco tinnunculus*)
Buzzard (*Buteo buteo*)
Sparrow hawk (*Accipiter nisus*)
Heron (*Ardea cinerea*)
Ring dove or wood pigeon (*Columba palumbus*)
Stock dove (*Columba oenas*)
Turtle dove (*Streptopelia turtur*)
Woodcock (*Scolopax rusticola*)
Moorhen (*Gallinula chloropus*)
Capercaillie (*Tetrao urogallus*)
Blackcock (*Lyrurus tetrix*)
Pheasant (*Phasianus colchicus*)

4. DEFINITION OF A WOODLAND BIRD

In this enquiry, observers were asked to record every bird which they saw in the woods that they investigated, and nearly all these species are recorded in the tabulated counts in the Appendix. However, to save space the sporadic records of species, such as the meadow pipit, which are typical of open ground without trees, and whose occurrence in woods is accidental and without significance, were omitted from these counts.

A further group of species was included in the Appendix, but are omitted from all detailed analysis in the present paper since, though they typically frequent trees or scrub, they are not typical of woods, and, when they occur

there, are almost exclusively on the wood edge. They are typical of open country with scattered trees or scrub, and are hardly to be considered woodland birds.

Table 1. *Species of the wood edge omitted from further consideration*

Magpie*	Woodlark
Greenfinch	Lesser whitethroat
Goldfinch	Wryneck
Tree sparrow	Cuckoo*
Yellow bunting	Turtle dove*
Cirl bunting	

* Magpie, cuckoo and turtle dove are fairly common in woods, but, like the rest, are *primarily* birds of more open country.

It should be emphasized that only a very arbitrary line can be drawn between those species which were omitted and those included. A "woodland bird" cannot be strictly defined, and other workers might make a different division. The birds of open country with scattered trees given in Table 1 grade insensibly into those frequenting parkland, with well-spaced trees at regular intervals, and so to those of very open woods. Again, certain "woodland" species, such as the tree pipit and various birds of prey, require only a single tall tree (either as a song post or for nesting), and so should not perhaps be included as woodland birds. But such of these birds as also occur regularly when there is more than one tree have been included as woodland birds in this paper. Again, a number of species obtain only some of their requirements, or a single one, in the wood, and other requirements, e.g. food, exclusively outside the wood. The occurrence of various species in woods is correlated with very different factors, and some of these species commonly, others only rarely, find all these requirements satisfied in situations outside woods. Even so typical a woodland species as the blackbird breeds in treeless areas in Shetland (Venables) and on Ailsa Craig (J. Fisher), feeding on grass moor, nesting in sheltered cracks or ledges in stone walls and rock-sides, and singing from the tops of stone walls and crags; all its requirements are satisfied without a single tree. Another difficulty is presented by such species as willow warbler and wren, which are really scrubland species; but since most scrubland in Britain to-day is found in woods, these are two of the commonest birds in woods; but they do not require any trees in their habitat, though they may use them when present. Hence it is difficult to say whether they should be considered as woodland birds.

It is clear that the term "woodland bird" is an artificial one. Different species of birds have different requirements, and these are satisfied to a greater or less degree by the habitat we term a wood. Probably, in earlier times, the birds of the natural forest land would have been much more sharply divided from those of other natural habitats, though there would still have been some overlap. But in Britain to-day there is almost no surviving natural forest

land, and the birds of the planted woodlands are not at all clearly demarcated from those of other man-made habitats such as orchards, gardens, parks, and hedgerows with tall trees.

5. THE REQUIREMENTS OF WOODLAND BIRDS

The requirements of the different woodland species are set out in Table 3. It saves space to tabulate separately those species which feed almost exclusively outside woods but which use trees (sometimes but by no means always in woods) for nesting sites. The requirement of these species is not a wood but one or more tall trees.

Table 2. *Species nesting in trees and feeding outside woods*

Rook	Hobby
Little owl	Heron
Kestrel	

N.B. Quite a number of other British birds occasionally nest in trees; only the most regular species have been included in Table 2.

Of the species in Table 2, the kestrel also breeds regularly on cliffs and the little owl in many types of holes outside woods, e.g. rabbit burrows. Rook and heron, being social, usually nest in a group of trees, both in woods and in isolated clumps. The hobby, which nests much more frequently in conifers than in broad-leaved trees, is essentially a bird of open country with trees, but does sometimes nest in woods. Hence some of these species might not be considered "woodland birds". Once again there is only an arbitrary line between these and such species as carrion and hooded crows, jackdaw, starling, stock and ring doves; all the latter have been included in Table 3, for though all of them except the ring dove breed commonly away from trees in some areas, when they do occur in woods they obtain much of their food there.

In Table 3 the requirements and niches of the different species have been classified so far as at present known, as these are essential for the appreciation of the later sections. The most fundamental divisions of the wood are the leaf canopy, the timber (by which is meant the trunk and main branches), the secondary growth, the ground, and the air between the canopy and the ground. *In Table 3 only those niches frequented most characteristically by each species have been tabulated.* If occasional or exceptional records were included, many more crosses would have to be added in each column, and this would destroy the typical picture which Table 3 is intended to present.

For a fuller ecological picture, both the food and the winter roosting places should have been added. Neither of these was made an object of the present enquiry. Much information on the food of British birds is available in the works of Collinge (**1**), Jourdain (**3**) and others. In many species too little is known about roosting for any generalizations to be made. The table shows the great diversity in the requirements of the various woodland species.

Table 3. *Typical niches of woodland birds*

Species	Breeding season														Winter				Remarks
	Nests				Sings*					Feeds					Feeds				
	Canopy	Holes	Secondary	Ground	Air	Canopy	Timber	Secondary	Ground	Air	Canopy	Timber	Secondary	Ground	Canopy	Timber	Secondary	Ground	
Carrion crow	×	.	.	.	×	×	.	.	.	.	×	.	.	×	.	.	.	×	—
Hooded crow	×	.	.	.	×	×	.	.	.	.	×	.	.	×	—	—	—	—	Not in woods in winter. Commonly breeds in rocks
Jackdaw	.	×	.	.	.	.	.	.	.	.	×	.	.	×	.	.	.	×	Occasional canopy nester. Also commonly breeds outside woods
Jay	×	.	×	.	.	.	.	.	.	.	×	.	×	.	×	.	×	×	Mainly in broad-leaved woods
Starling	.	×	.	.	.	×	.	.	.	×	×	.	.	×	.	.	.	×	Common outside woods
Siskin	×	.	.	.	×	×	.	.	.	.	×	.	.	.	×	.	.	×	Summer in coniferous, winter in birch-alder
Chaffinch	×	.	×	.	.	×	.	×	.	.	×	.	×	×	.	.	.	×	All types of wood
Brambling	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.	.	.	×	Predominantly in beech in winter. In Scandinavia nests in pine and birch
Lesser redpoll	×	.	.	.	×	×	.	.	.	.	×	.	.	.	×	.	.	×	Predominantly in birch-alder
Hawfinch	×	.	.	.	.	×	.	×	.	.	×	.	×	×	×	.	×	×	—
Bullfinch	.	.	×	.	.	.	.	×	.	.	×	.	×	.	×	.	×	.	Scrub species
Crossbill	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	.	.	Wood edge for nesting. Conifer only. Near water
Tree pipit	.	.	.	×	×	×	.	.	.	.	.	.	.	×	—	—	—	—	Open woods
Tree creeper	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	.	Frequents small branches also. Nests in cracks in bark
Nuthatch	.	×	.	.	.	×	×	.	.	.	?	×	.	.	×	×	.	.	Predominantly in broad-leaved woods
Goldcrest	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	×	.	Predominantly in coniferous woods
Great tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	More numerous in broad-leaved woods
Coal tit	.	×	.	.	.	×	.	.	.	.	×	×	?	.	×	×	×	×	More numerous in conifer woods
Marsh tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	Predominantly in broad-leaved woods
Willow tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	Near marsh or water. Broad-leaved woods
Blue tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	More numerous in broad-leaved woods
Crested tit	.	×	.	.	.	×	.	.	.	.	×	.	.	.	×	×	×	×	Predominantly in coniferous woods
Long-tailed tit	.	.	×	.	.	×	.	×	.	.	×	.	×	.	×	.	×	.	Scrub species

Whitethroat	.	.	×	.	×	.	.	×	.	.	.	.	×	×	—	—	—	—	Scrub species
Garden warbler	.	.	×	.	.	×	.	×	.	.	×	.	×	×	—	—	—	—	Predominantly in broad-leaved woods
Blackcap	.	.	×	.	.	×	.	×	.	.	×	.	×	×	—	—	—	—	Predominantly in broad-leaved woods
Willow warbler	.	.	.	×	.	×	.	×	.	.	×	.	×	×	—	—	—	—	Scrub species
Wood warbler	.	.	.	×	×	×	.	.	.	.	×	.	×	×	—	—	—	—	Predominantly in broad-leaved woods with sparse or absent secondary growth
Chiffchaff	.	.	×	.	.	×	.	.	.	.	×	.	×	×	—	—	—	—	Mainly in broad-leaved woods
Mistle thrush	×	.	.	.	.	×	.	.	.	.	.	.	.	×	×	.	×	×	Nests in strong fork, often low down
Song thrush	.	.	×	.	.	×	.	×	.	.	.	.	.	×	×	.	×	×	—
Blackbird	.	.	×	×	.	×	.	×	.	.	.	.	.	×	×	.	×	×	—
Redstart	.	×	.	.	.	×	.	.	.	×	.	.	.	×	—	—	—	—	Open woods for "pouncing"
Robin	.	×	.	×	.	×	.	×	.	.	.	.	.	×	.	.	×	×	—
Nightingale	.	.	×	×	.	.	.	×	.	.	.	.	.	×	—	—	—	—	Predominantly in broad-leaved woods
Dunnock or hedge sparrow	.	.	×	.	.	.	.	×	.	.	.	.	×	×	.	.	.	×	Scrub species
Wren	.	×	×	×	.	.	.	×	.	.	.	.	×	×	.	.	×	×	Scrub species. Nests in any hole or crack. Also away from woods and scrub
Spotted flycatcher	.	×	.	.	.	×	.	×	.	×	.	.	.	.	—	—	—	—	Open woods for "pouncing". Nests in ledges or cracks
Great spotted woodpecker	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	.	All types of wood
Lesser spotted woodpecker	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	.	Predominantly in open broad-leaved woods
Green woodpecker	.	×	.	.	.	.	×	.	.	.	.	×	.	×	.	×	.	×	More numerous in broad-leaved woods
Nightjar	.	.	.	×	.	×	.	×	.	×	.	.	.	.	—	—	—	—	Open woods for "snapping". Bare earth for nest
Long-eared owl	×	.	.	.	.	×	.	.	.	×	.	.	.	.	.	.	.	.	
Tawny owl	.	×	.	.	.	×	.	.	.	×	.	.	.	.	.	.	.	.	Feeds on the wing
Sparrow hawk	×	.	.	.	×	.	.	.	.	×	.	.	.	.	.	.	.	.	
Woodcock	.	.	.	×	×	.	.	.	.	.	.	.	.	×	.	.	.	×	Nests near swamp or stream
Stock dove	.	×	.	.	.	×	.	.	.	.	.	.	.	×	.	.	.	×	Sometimes nests in rabbit holes outside woods, or in cliffs
Ring dove	×	.	×	.	.	×	.	.	.	.	×	.	.	×	×	.	.	×	All types of wood
Pheasant	.	.	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	Uses the trees for roosting
Capercaillie	.	.	.	×	.	×	.	.	.	.	×	.	.	×	×	.	.	.	Predominantly in coniferous woods
Blackcock	.	.	.	×	.	.	.	.	×	.	×	.	.	×	×	.	.	.	Open woods. Predominantly in pine and birch

* Or other breeding call.

6. Methods of survey

For describing and discussing woodland distributions, it was desirable to obtain a *comparative index* of the abundance of each species in the different wood types. Although total populations were not an object of the enquiry, the ideal method for obtaining such a comparative index was to have complete censuses taken of a large number of woods of each different type. But such complete censuses would have required an enormous quantity of extremely arduous work, and so few sample woods could have been taken that no generalizations on habitat distribution could have been safely made; nor did any of the various shorter methods for obtaining quantitative results, summarized by Lack (**5**), seem practicable under the circumstances of the present enquiry.

Another method was to ask observers to send in simply a list of all the species found in each wood, with no reference to frequency. On the assumption that the commoner a bird is the more woods it is likely to be recorded from, a comparative frequency index can be obtained from the percentage of woods in which each species occurs. This gives an index of some value, but it was obviously preferable if observers could give some indication of relative abundance. Terms such as common and rare are worse than useless, since they have different meanings for different observers and different species. Therefore each observer was asked to record the actual numbers of each species that he observed during a slow walk through the wood. Where possible, one or more counts were taken later, and in such cases the figure for each species in the Appendix is the largest number of individuals of each species seen on any one walk.

The figures obtained on one sample walk are obviously only a very rough indication of the numerical abundance of the different species. A second count taken soon after the first along the same route often shows considerable differences from the first. Hence the figures must not be used too precisely. Nevertheless, they do present an advance on the bare species list. With these considerations in mind, a comparative index of abundance for each species was obtained as follows. Where only one individual of a species was seen in the walk or walks through a wood it was scored as 1, between two and nine individuals were scored as 2, and over nine were scored as 3. The score of each species in all the woods of the same type was added, and, to make the figures for the different woods comparable, this score was then divided by the number of woods involved. To make a suitable index, the highest number obtained by this method, namely, 2·6 for the chaffinch in Highland pine, was taken as 100, and the other index numbers were calculated in proportion, which means multiplying them by 37·5. The results are given to the nearest ten. Table 4 gives the results.

The method of calculating the index from the figures in the Appendix will be clearer from an example. In the breeding season counts of the 45 oak and

mixed broad-leaved woods, the great tit was recorded singly 6 times (score 6), between 2 and 9 individuals were recorded 21 times (score 42), and over 9 individuals were recorded once (score 3). The total score is therefore $6+42+3=51$. This number is divided by the number of woods, namely, 45, and multiplied by 37·5 to make a suitable index, which gives a figure of 40 when expressed to the nearest 10. In the breeding season counts for pine woods, the index for the great tit works out at 10. From this it may reasonably be inferred that the great tit is roughly four times as abundant in oak woods as pine woods in the breeding season. A similar calculation for the coal tit gives an index of 20 for oak woods and 60 for pine woods, in the breeding season; hence this species shows a frequency as regards oak and pine woods which is almost the reverse of that of the great tit.

The reason for assessing the number of individuals recorded on each count in three arbitrary divisions, scoring respectively 1, 2 and 3, was as follows. Even in the breeding season, woodland birds wander to some extent, hence, if only one individual was seen, it might well be sporadic, and such a record clearly has less value than if two or more individuals were seen, which suggests regularity. The counts were obviously not sufficiently accurate to be treated as they stood, hence all figures between 2 and 9 were grouped together, and were scored as 2. On the other hand, if 10 or more individuals were seen, that species was clearly abundant, and so was scored as 3.

Since a large number of woods of each type was counted, it is claimed that the comparative index of abundance obtained as described does present a fairly accurate picture of British woodland bird distributions, and this picture corresponds with the impressions of the present writers without the subjective errors to which the latter, by themselves, would be liable. To avoid confusion, it should be reiterated that the figures in the Appendix are not complete censuses, and that no greater accuracy is claimed for them than what is needed for obtaining the comparative index as described; while only major differences in comparative index are considered in the subsequent discussion. No method is available for testing the reliability of the index except by taking complete censuses of all the woods concerned. For a closer analysis of habitat distributions, a single group of species might be selected, for which complete censuses might well be practicable, but, as already stated, the object of the present enquiry was a general survey.

When the figures are treated to get only the most obvious differences, as described, one error remains, namely, that certain species, notably the tree-creeper, are less conspicuous than others, and so are relatively too few in the counts. For this reason the counts are used primarily for comparing the distributions of the same species in different habitats, not of different species in the same habitat.

Observers were asked to investigate woods of as pure types as possible (but a few counts from mixed woods were included in the Appendix), and detailed

descriptions of the actual woods counted by each observer have been deposited at Oxford with the British Trust for Ornithology, where those interested can consult them. To save space, only more generalized descriptions are given here.

Counts were taken in both the breeding and the non-breeding season, the former between mid-April and June (at least two counts where possible), the latter for convenience restricted to between November and February. Altogether 152 woods were counted in summer and 120 in winter, of which the two writers themselves counted 50 in summer and 61 in winter. This paper is based not only on these counts, but also on the writers' observations in many other woods, while questions on which further information was required were circulated among a group of experienced field observers.

Discussion of Table 4

Ideally the indices should have been tabulated in a number of separate tables, one in each relevant section of the following discussion, but, on account of space considerations, they have all been placed in one table, in a number of separate sections. Therefore in reading the following discussion, Table 4 should be constantly referred to, as actual figures are not quoted again in the text. While most of the discussion is based on Table 4 (also supported by the general field impressions of the writers), the influence of certain factors, also the distribution of certain uncommon species, cannot be worked out from indices based on the observers' counts. The evidence in these cases is based on the field observations of the present writers together with those of the members of the scientific advisory committee of the British Trust for Ornithology; such cases are clearly specified in the text.

The whole of the first part of the discussion refers exclusively to the breeding season, winter distributions being considered separately at the end.

As shown in Table 4, a few species, notably chaffinch and ring dove, and to a lesser extent tree creeper, mistle thrush, robin and great spotted woodpecker, occur almost equally in all types of woods during the breeding season. But there are quite marked differences in the bird species of the different kinds of woods. Some of these differences seem correlated directly with the species of tree composing the wood, but several other factors are extremely important, and these will be considered first.

7. Some habitat factors

(*a*) *Birds of open as opposed to closed woods*

Certain species of woodland birds occur predominantly in woods where the trees are widely spaced, and when they do occur in woods with a closed canopy are found predominantly on the edges and near rides. It is, naturally, impossible

Table 4. *Comparative index of frequency of woodland birds in different wood types**

	Breeding season											Winter			
	Oak and five mixed broad-leaved	Beech	Birch	Pine and one pine with larch	Larch	Pine – secondary	Pine – secondary	Oak and beech – secondary	Oak and beech – secondary	Pine forest (Highlands)	Pine plantations	Oak and two mixed broad-leaved	Beech	Birch	Pine and one pine with larch
Number of woods ...	45	24	22	33	11	16	17	56	13	9	24	39	18	17	33
Carrion crow	10	·	5	10	10	10	10	10		10	10	10	—	—	—
Hooded crow	—	—	—	5	—	—	10	—	—	20	—	—	—	—	—
Jackdaw	10	30	10	—	—	—	—	10	20	—	—	10	5	—	—
Jay	30	20	5	10	20	10	×	30	×	—	10	40	20	10	20
Starling	10	60	10	5	—	5	10	40	50	—	10	10	10	—	×
Siskin	—	—		10	—	10	×	—	—	30	—	—	—	10	—
Chaffinch	70	60	70	90	90	80	90	60	70	100	80	30	90	20	10
Brambling	—	—	—		—	—	—	—	—	—	—	—	60	—	×
Redpoll	—	×	10	×	—	×	—	—	—	—	×	10	—	50	×
Bullfinch	20	10	5	×	×	×	—	20	—	—	×	20	10	40	5
Crossbill	—	—	—	10	—	10	20	—	—	20	10	—	—	—	20
Tree pipit	·	5	10	10	—	10	20	×	10	40	×	—	—	—	—
Tree creeper	10	20	10	10	30	10	10	10	×	20	10	20	20	5	30
Nuthatch	10	10	×	—	—	—	—	10	5	—	—	20	20	×	—
Goldcrest	5	(5)†	×	50	40	60	40	5	—	50	50	30	—	20	80
Great tit	40	30	20	10	30	20	10	40	20	—	20	50	60	40	10
Coal tit	20	20	30	60	60	70	60	30	×	80	60	40	40	30	80
Marsh + willow tits‡	20	20	20	—	10	—	—	20	10	—	—	50	30	×	10
Blue tit	50	30	40	10	50	10	5	50	10	—	10	70	80	70	30
Crested tit	—	—	—	10	—	10	10	—	—	50	—	—	—	—	10
Long-tailed tit	20	5	10	5	×	5	5	20	—	—	5	50	20	30	10
Whitethroat	30	5	10	5	—	10	—	30	—	—	10	—	—	—	—
Garden warbler	20	10	10	5	×	10	—	20	—	—	5	—	—	—	—
Blackcap	20	10	5	5	×	10	—	20	×	—	10	—	—	—	—
Willow warbler	70	20	80	30	50	50	20	60	—	30	30	—	—	—	—
Wood warbler	10	30	10	×	—	—	×	10	50	—	×	—	—	—	—
Chiffchaff	30	30	10	×	30	5	—	40	—	—	5	—	—	—	—
Mistle thrush	30	20	10	20	×	20	20	30	10	10	30	10	10	—	5
Song thrush	50	40	30	10	30	20	10	50	20	10	10	30	20	10	5
Blackbird	70	70	50	30	50	40	20	70	50	×	40	70	60	20	20
Redstart	×	10	5	20	—	10	20	5	·	50	5	—	—	—	—
Robin	60	50	60	30	50	60	20	60	40	40	30	60	30	30	10
Nightingale	10	5	×	×	—	×	—	10	—	—	×	—	—	—	—
Dunnock or hedge sparrow	20	10	10	10	10	30	—	20	—	×	20	30	10	20	10
Wren	60	30	30	30	30	40	10	50	20	10	30	40	20	20	30
Spotted flycatcher	5	10	5	×	—	5	—	10	10	×	5	—	—	—	—
Great spotted woodpecker	10	10	5	5	×	10	×	10	×	—	10	10	×	5	5
Lesser spotted woodpecker	5	5	×	—	—	—	—	5	×	—	—	5	—	—	—
Green woodpecker	10	20	10	5	10	10	—	20	10	—	5	10	10	10	10
Woodcock	5	—	10	×	—	5	—	×	5	×	×	10	—	10	—
Stock dove	5	10	5	10	—	10	10	10	×	—	20	×	—	—	—
Ring dove	40	60	40	40	70	50	40	50	50	×	60	50	80	20	20
Pheasant	30	10	10	20	20	30	10	30	×	10	20	30	10	5	10
Capercaillie	×	—	—	10	—	20	5	—	5	30	5	—	—	×	10
Black grouse	—	—	10	10	—	×	20	—	—	30	—	—	—	×	5

* The method of obtaining the index is described on pp. 46-7. × indicates a score of 1 whatever the calculated index. A single occurrence is liable to be sporadic. 5 indicates an index of between 3 and 7 when there was more than one occurrence. 10 indicates an index of between 7 and 14. All other indices are calculated to the nearest 10.

† Four goldcrests recorded from beech woods in June had probably moved in after breeding, so this should probably be blank. [N.B. Those in oak woods were breeding.]

‡ Marsh and willow tits were not distinguished by many observers, so were scored together.

to draw any clear line between these species and those given in Table 1, which were so much birds of the wood edge as to be omitted from further consideration. But all the birds characteristic of open woods given in the following list occur regularly right into the interior of woods, provided there is an open canopy:[1]

Crossbill	Pied flycatcher
Tree pipit	Lesser spotted woodpecker
Wood warbler	Nightjar
Redstart	Blackcock
Spotted flycatcher	

The tree pipit was the only one of these species invariably recorded from a wood with an open as opposed to a closed canopy. Like the woodlark, it has an aerial song flight from a high perch, and Lack (**4**) and Venables (**15**) show that a high song post is the only factor for which these species require trees. Redstart, spotted and pied flycatchers, and nightjar, when not in woods with an open canopy, require much open space between canopy and secondary growth; in this they catch their insect food on the wing. The nightjar is regular in woods, but also on heathland; the presence of a wood seems immaterial to it, though it uses tall trees for singing and roosting when these are available. The wood warbler should not perhaps have been included in this group. It needs "space", but is characteristic not of woods with an open canopy, but of woods with a closed high canopy with almost no secondary or undergrowth; when it does occur in woods with secondary growth there is nearly always much space between canopy and secondary growth. In this it agrees with the redstart and the flycatchers, but its distribution is correlated not with feeding but with its habit of an aerial song flight from one bough to the next. The black grouse seeks the cover of trees when disturbed, and at times feeds in them, but it also feeds regularly in open country, and normally displays on flat open ground devoid of trees. Crossbill and lesser spotted woodpecker are typical of open woods, but this does not seem correlated with any special habits or adaptations.

(*b*) *Birds dependent on secondary growth*

The term "secondary growth" cannot be precisely defined, since it grades into tall ground vegetation on the one hand and low trees on the other. The term is used here for the bushes, scrub and young trees found as a layer below the canopy trees in many woods, and from 3 to 12 ft. may be taken as its usual height.

In one section of Table 4, indices are calculated separately for birds in

[1] This list is based on the writers' experience. It was impossible to separate out the open from the closed woods from the observers' lists, as so many woods included both open and closed parts, so that index figures could not be compiled. In the observers' counts (Appendix) it may be noted that among pine woods, A 28, 29, 30, 31, 48 and 49 had open canopy throughout, and that all Scottish and North of England birch woods have a predominantly open canopy.

woods with secondary growth and in woods without secondary growth. for both coniferous and broad-leaved woods. It should be noted that almost no wood is completely devoid of secondary growth, hence a few birds typical of secondary growth were recorded in woods classified as without secondary, and some of the woods with secondary growth had some areas without any. Hence the differences dependent on secondary growth are really more marked than this table indicates. (Woods containing young trees and trees with low branches were, of course, included as woods with secondary; hence no birch woods were included as without secondary.)

Table 4 shows clearly that the following species occur typically in woods with good secondary growth and not where this is absent.

Jay	Chiffchaff
Bullfinch	Nightingale
Long-tailed tit	Dunnock or hedge sparrow
Whitethroat	Wren
Garden warbler	Pheasant
Blackcap	Capercaillie
Willow warbler	

The height of secondary growth required differs for the different species (based on field observations). Wren, pheasant and capercaillie require tall ground vegetation rather than secondary growth. Most of the others require secondary growth at least about 4 ft. high, the nightingale and garden warbler at least about 8 ft. and the jay typically higher than these. At this stage other species, such as robin and song thrush, might have been included. The series grades into species frequenting lower trees, so that no definite line can be drawn. (For the stage at which different species colonize trees of different heights see the studies of young plantations by Schiermann (**12**), and Lack (**4**).)

Of the thirteen species in the above list, nine are typical of scrub or secondary growth (of the heights already given) outside woods, and so are not dependent on woods as such. Of these nine species five, namely, bullfinch, whitethroat, nightingale, dunnock and wren, *tend* to keep mainly in the secondary growth for all their activities in the breeding season even when they are nesting in woods. Of the other four species, the long-tailed tit feeds in the trees, the pheasant roosts there and garden and willow warblers sing (and to some extent feed) there, when they breed in woods, but for none of these are canopy trees essential. But blackcap and chiffchaff, unlike their relatives the garden warbler and willow warbler respectively, do not occur in scrub outside woods unless there are also a few tall trees. For these two species one (and, at least for the blackcap apparently, only one) essential requirement is supplied by woods, namely, the tall song posts afforded by canopy trees. Although both blackcap and chiffchaff at times sing lower down in their territories, each territory investigated had some taller song posts, hence these species are found typically only in woods; whereas the minimum height of song post required by garden and willow warblers is satisfied by secondary growth. Blackcap and

chiffchaff utilize secondary growth for nesting, also for cover and feeding; the chiffchaff also feeds a great deal in the canopy. The remaining two species, jay and capercaillie, are arboreal in many of their habits, and do not occur in secondary growth outside woods.

The species discussed above are almost confined to woods with good secondary growth. Table 4 shows that although some other species are commoner in such woods, they also occur, though less frequently, in woods without secondary growth. This is true of the hole-nesting tits which are also commoner in open woods without secondary growth (including parks) than in closed woods. Song thrush and robin are also commoner in, but by no means confined to, woods with good secondary growth, the former nesting in it, the latter using it for feeding and cover. The robin, like the wren, also occurs in woods devoid of secondary growth when there are rocks or stone walls, which they use for nesting and also feeding. The wren even occurs in many rocky areas devoid of both trees and bushes.

Table 4 also shows three species to be much commoner in woods devoid of secondary growth than in woods where it is present, namely, tree pipit, wood warbler and redstart. The tree pipit, except for its tall song post, is essentially a ground bird, like the meadow pipit. Wood warbler and redstart have already been discussed; they do occur in woods with secondary growth, but require much open space, hence are commoner in woods where secondary growth is scarce. Not enough figures were available for the nightjar, but it also is typical of woods without secondary growth. In addition to requiring much space for feeding, it also nests on bare ground.

(c) *Hole-nesting birds*

The following species nest in holes and are therefore scarce in or absent from younger plantations and are particularly common where there are old trees:

Jackdaw	Crested tit
Starling	Redstart
Tree creeper (cracks)	Spotted flycatcher (ledges)
Nuthatch	Pied flycatcher
Great tit	Great spotted woodpecker
Coal tit	Lesser spotted woodpecker
Marsh tit	Green woodpecker
Willow tit	Tawny owl
Blue tit	Stock dove

(Also tree sparrow and wryneck in Table 1, and little owl in Table 2.)

Of the above species, jackdaw, starling and stock dove, and, to a lesser extent, the tawny owl, regularly nest outside woods in other kinds of holes. The others are more truly woodland birds; but many of them will nest in artificial holes in woodwork (especially in nesting boxes or holes in buildings), and nuthatch, coal, marsh and blue tits nest occasionally in holes in stonework. The

coal tit also nests not infrequently in holes in banks or even in the flat ground, and for this reason is found in certain woods not frequented by the other hole-nesting tits.

(*d*) *Birds dependent on tall trees*

A number of species normally nest only in tall trees in the canopy, and hence are absent from woods which do not possess at least one such tall tree. The species primarily concerned are the canopy-nesting Corvidae and Falconidae (set out in Tables 2 and 3). The height of the tree required is rather different for the different species, and also shows local variations in the same species; for instance, on Dartmoor the carrion crow regularly breeds in stunted wind-bent trees, these nests being much lower than in the lowlands a few miles away. The other canopy nesters can be seen from Table 3; most of them require rather lower trees than the Corvidae and Falconidae, each species having a typical minimum height, though most species will nest lower than this in special circumstances.

For other species, tall trees are essential as song posts. Here again, the minimum height varies with the species, and seems rather more rigidly adhered to than in the case of nesting height. The crossbill, tree pipit, blackcap, chiffchaff, mistle thrush, redstart and ring dove may be specially mentioned, but these grade insensibly into species whose minimum height of song post is satisfied in high or low secondary growth. In some of these species, notably tree pipit, blackcap, chiffchaff and redstart, the sole factor essentially supplied by the canopy, and hence by woods, is a tall song post, all the other activities (nesting, feeding, etc.) of these birds occurring predominantly either in the timber, secondary growth, on the ground or in the air. This section is based on the writers' experience. Though observers recorded the height of the trees in their woods, it was not possible from the figures sent in to give any comparative frequency indices for woods of different heights. Too many woods contained trees of variable heights. This aspect is, however, studied in the plantation studies of Schiermann (**12**) and Lack (**4**).

(*e*) *Birds dependent on water*

The presence of water brings various aquatic or marsh species into woods—and the grey wagtail then uses trees as song posts, the moorhen for nesting—but such species need not be considered here. One true woodland species, the woodcock, typically breeds near a marsh or stream, by which it feeds. It is interesting that neither trees nor secondary growth are utilized in any of its activities by this predominantly woodland wading bird, which nests in thick ground vegetation and displays in the air. Possibly it gains by the cover afforded by woods, and its rounded wings, unusual in a wader, seem adapted to woods. It does occasionally nest away from woods.

The crossbill usually nests close to water; it seems to drink more than other

birds, perhaps on account of its relatively drier food. The willow tit breeds almost exclusively in damp woods or near water, a habit which it is difficult to correlate with any adaptation or particular activity. Possibly it is connected solely with its need for a nesting hole, which is typically in soft wood excavated by the bird. Such soft, rotten wood is much commoner near water. The species occasionally breeds right away from water, e.g. on the chalk downs (E. M. Nicholson, Venables). The pied flycatcher also occurs regularly along streams, but is by no means confined to such haunts: stream edges provide an open habitat for its "pouncing" feeding habits.

8. Comparison of communities in different woodland types

(*a*) *Broad-leaved deciduous woods, excluding birch*

The typical British oak wood (*Quercus robur* or *sessiliflora*) is only moderately closed, allowing a fair amount of light to penetrate inside the wood. There is usually a slight admixture of other broad-leaved trees, particularly ash (*Fraxinus excelsior*), elm (*Ulmus*) and sycamore (*Acer pseudoplatanus*). (Where the wood also contained conifers, either the count was omitted or, if the conifers were extremely local, the observer omitted that part of the wood from his count.)

There is typically a rich, varied but often patchy secondary growth of deciduous bushes, mainly hazel (*Corylus avellana*), elder (*Sambucus nigra*), hawthorn (*Crataegus*), and saplings of trees, with a few evergreens such as holly (*Ilex aquifolium*), ivy (*Hedera helix*) and *Rhododendron*. There is a varied ground vegetation in which bramble (*Rubus*), bluebell (*Scilla non-scripta*), and bracken (*Pteridium aquilinum*) are conspicuous, together with many other species.

Though most British oak woods are planted, the trees are usually permitted to grow fairly old, hence nesting holes are usually present.

In the recorded counts, nearly all the woods conformed to this type. M 1 to M 5 had many canopy trees of deciduous species other than oak, but were otherwise extremely similar in type, so were included with the oak woods for the indices. H 37 and H 38 were old plantations in which secondary growth was absent. H 39 was oak coppice 18 ft. high, with no secondary growth, no nesting holes and very few forks suitable for nests. H 40 was an extremely isolated wood on Dartmoor, with gnarled stunted trees, no secondary growth, but with rocks and good ground vegetation.

The typical south of England oak or mixed broad-leaved deciduous wood is richer in bird life than any other type of British woodland; but many of the differences between this type and the typical pine woods of Southern England are really correlated with the presence in the former of rich secondary growth, old trees with holes, and comparatively wide spaces between the trees, all of

Phot. H. N. Southern

Phot. 1. Typical oak-mixed broad-leaved wood, showing rich ground vegetation of bracken in foreground and secondary growth of deciduous bushes behind.

Phot. L. S. V. Venables

Phot. 2. Typical older pine plantation, with bare trunks, high canopy and no secondary growth.

which features are absent from the typical pine plantation. On the edge of Dartmoor are a number of closely planted oak coppice woods, with no secondary growth and no old trees or holes. Here the summer population consists typically of only a few jay, chaffinch, willow and wood warbler, robin and ring dove, which is quite as poor an avifauna as that of the typical older pine plantation (Lack; see also H 39).

The typical oak and mixed broad-leaved wood with good secondary growth contains all the characteristic British woodland species except the few mentioned later as confined to conifer woods or birch. As is very clear from Table 4, the following species breed predominantly in oak and mixed broad-leaved woods and breed at most rarely in pure pine woods even when the latter provide secondary growth (coniferous), nesting holes and open woodland:

Nuthatch	Chiffchaff
Marsh tit	Nightingale
Garden warbler	Spotted flycatcher
Blackcap	Lesser spotted woodpecker
Wood warbler	

Of these species, nuthatch, marsh tit and lesser spotted woodpecker were not recorded breeding in pure coniferous woods at all. However, the last is a scarce bird and does at times frequent coniferous forest in northern Europe (B. W. Tucker). The nuthatch (a different race) also frequents conifer forest in parts of Switzerland (B. W. Tucker). Garden warbler and blackcap occurred occasionally in woods with exclusively coniferous trees but broad-leaved deciduous secondary growth, cases which do not strictly constitute an exception. In addition they occurred rarely in pine woods with no broad-leaved secondary growth on the Norfolk Breckland, as did the chiffchaff and (once) the nightingale (there was one small patch of widely spaced 2 ft. deciduous saplings in the birds' territory). The chiffchaff also breeds occasionally in pure yew scrub (Venables). The wood warbler is scarce but regular in pure pinewoods in Surrey. For the spotted flycatcher the data provided by the enquiry are hardly adequate. It is mainly a bird of the wood edge, but was not recorded from any purely coniferous woods, though it nested on a pine in one mixed wood. However, since it frequents open coniferous woods on the European mainland (B. W. Tucker, F. C. R. Jourdain), its apparent absence from British ones may be due mainly to the scarcity of suitable nesting ledges in the pine plantations of the south of England. One further species, the hawfinch, is typical of broad-leaved woods (oak and beech) and has not been recorded from coniferous woods; it is a secretive species and was recorded too seldom for inclusion in Table 4.

The following additional species typical of oak and mixed broad-leaved woods are regular but definitely much less common (to a varying degree, see Table 4) in pure pine woods:

Bullfinch	Blue tit
Great tit	Green woodpecker

In addition to these, the willow tit (typical of birch woods) breeds regularly in damp oak woods and is absent from pine woods unless these contain stream or marsh side alder or birch stumps. These conclusions are based on data from experienced field observers, not from Table 4, as so many observers cannot distinguish this species from the marsh tit.

The apparent scarcity or absence of the jackdaw and starling from pure coniferous woods is perhaps correlated entirely with the absence of suitable nesting holes in most pine plantations; both nest in pine woods occasionally, hence they were omitted from the above two lists.

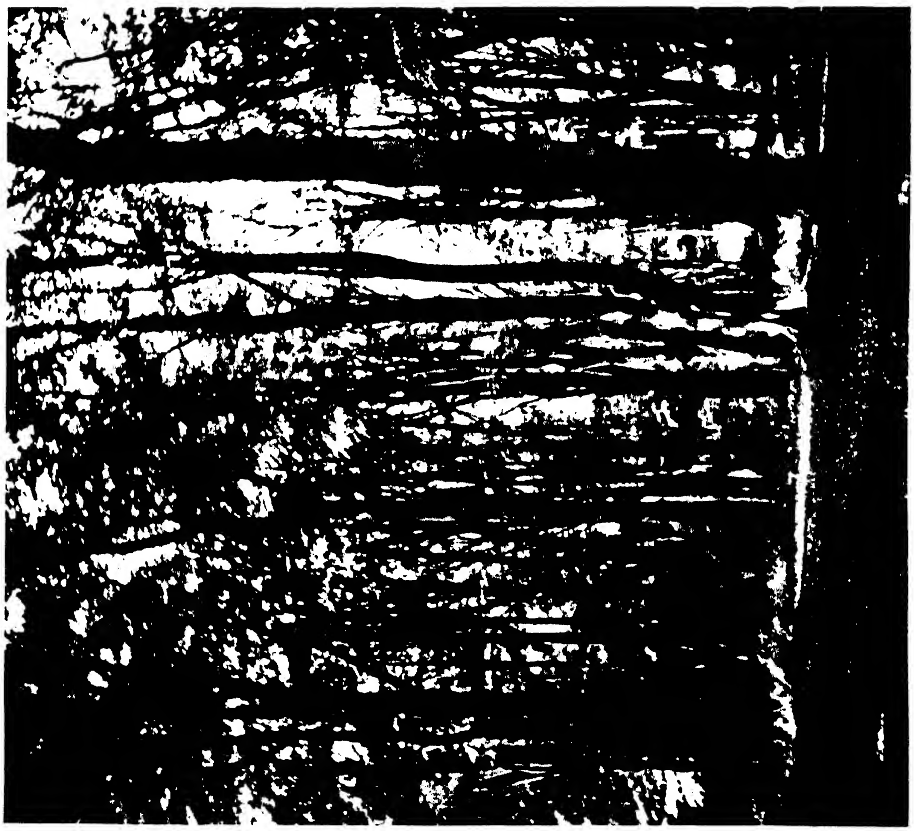
The writers have not been able to associate the predominance of the species in these lists in broad-leaved as opposed to coniferous woods with any particular habit or adaptation, except in the case of the nightingale, which builds its nest with dead deciduous leaves. It might be thought that the scarcity of certain warblers in conifers was correlated with the scarcity of secondary growth in English conifer woods, but the Breckland pine plantations provide good secondary growth where some warblers, but not those on these lists, are common. Further, the wood warbler avoids woods with secondary growth, yet is scarce in pine plantations. Alternatively, it might be thought that the scarcity of the warblers in coniferous as compared with broad-leaved woods was correlated with differences in the insect fauna. But all the warblers seem to have an extremely varied insectivorous diet, and here again certain species, but not the others, seem successful in pure pine woods. A further difficulty is that some birds e.g. nuthatch, lesser spotted woodpecker, occur in coniferous woods in other parts of their European range.

(*b*) *Beech woods*

The typical British beech wood (*Fagus sylvaticus*) is moderately closely planted, with a closed high canopy. Secondary growth is typically absent, but is often thick on the edges and in occasional open spaces, and is present (particularly evergreens such as holly, or box (*Buxus sempervirens*) within some woods, though then usually sparse. The woods marked + in the Appendix contained some of such secondary growth, but in nearly all of them much of the wood was devoid of secondary growth. Those marked – had almost no secondary growth at all. Since the trees are usually allowed to reach a considerable age, nesting holes are typically numerous. Ground vegetation is often absent, though there may be moss and sparse grass; the ground is often covered with dead leaves and, in winter, beech mast. All the woods counted were pure or almost pure beech except for J 12, which was predominantly beech but contained some oak and sycamore.

The birds of beech woods with good secondary growth show no diagnostic differences from those of oak and mixed broad-leaved woods, but since in the typical beech plantation secondary growth and ground vegetation are scarce

Phot. 2. Typical Highland birch wood. Trees well spaced, secondary growth of younger birch. (K 17 of Appendix.)



Phot. H. Reid Kerr

Phot. 1. Typical British beech wood: showing scarcity of ground vegetation and secondary growth. (J 2 of Appendix.)

or absent and holes are specially common, the wood warbler and all hole-nesting species are relatively commoner, and birds dependent on secondary growth are relatively scarcer than in typical oak woods.

(c) *Birch woods*

Typical British birch (*Betula*) woods are found mainly between the north of England and the Scottish Highlands. Those counted were normally open or moderately open, with a deep canopy, and contained fairly old trees and numerous nesting holes. Secondary growth was predominantly birch saplings, with juniper (*Juniperus communis*) in most of the Highland woods, and very occasional gorse (*Ulex europaeus*), hawthorn and elder in various others. The few birch woods counted in the south of England had young trees in close formation, while nesting holes were scarce or absent.

The four mixed birch woods were predominantly birch; L 1 had a few ash and oak, L 2 a number of willows (*Salix*) and rich secondary of the same, and L 3 alders (*Alnus rotundifolia*).

On the whole, the birds of birch woods are similar to those of other broad-leaved types. Three species are specially characteristic of birch woods:

Lesser redpoll	Black grouse
Willow tit	

As shown in Table 4, the lesser redpoll breeds predominantly in birch and in no other wood types; however, it breeds occasionally in pure pine woods, and, especially in gardens in the south of England, nests in many other kinds of trees. The willow tit (whose distribution, as noted, cannot be assessed from Table 4) is typical of birch woods, and is also fairly regular in oak and mixed deciduous woods usually near water. The black grouse is regular in both birch and pine, probably being commoner in the latter; birch is the only type of wood with broad-leaved trees in which it is regular.

Table 4 also shows that certain species are relatively scarcer in birch woods than in other broad-leaved types. This applies to a number of the species which nest in secondary growth. The secondary growth of birch woods is chiefly young birch, and this affords much less suitable nesting sites than typical broad-leaved secondary growth, except for the lesser redpoll, which builds an extremely small nest. It is therefore of interest that one species typical of secondary growth, the willow warbler, is just as common in birch as in typical broad-leaved woods; unlike the other species it is dependent on secondary growth not for nesting (it nests on the ground) but for singing and cover, for which birch seems adequate. From Table 4, jay, nuthatch and green woodpecker would also seem scarcer in birch woods than in other broad-leaved types. This may, however, be a geographical question. Most of the older birch woods counted were too far north for nuthatch and green woodpecker, and the jay

was absent from the region where the Highland counts were taken. If more mature birch woods occurred in the south of England, these three species might be more regular in birch woods.

(*d*) *Other broad-leaved woods*

A few broad-leaved woods of other species were counted. N 1, N 2, N 4, N 5, N 6 and N 8 were young plantations of the species given in the headings, the trees planted close together and secondary growth, where present at all, rather sparse; nesting holes were absent. N 3 and N 7 were old apple (*Pyrus communis*) orchards with widely spaced trees, locally thick secondary growth of hawthorn and willow, and grass below. N 9 was an alder plantation of fairly old trees with a little secondary growth, in marshy ground. O 1, O 2, and O 3 were typical hawthorn scrub.

As is apparent from the Appendix, closely grown young broad-leaved plantations of various species (oak, birch, sweet chestnut (*Castanea sativa*), etc.) are extremely poor in birds; indeed sometimes such plantations have no breeding birds at all. They provide no nesting holes, and, as compared with young pine plantations, the cover and branches are extremely sparse, affording few nesting sites. Apple orchards have, when the trees are old, a fairly rich avifauna, similar to that of parkland. Hawthorn scrub is rich in the birds dependent on secondary growth, but this strictly comes outside the scope of this paper.

(*e*) *Pine woods*

The Scots pine (*Pinus sylvestris*) woods fall into three distinct groups. Those marked H are parts of the natural pine forest still surviving in the Spey valley, in the Scottish Highlands. They consist of old and young trees, well spaced, so that much light gets in, the branches growing to low down on the trees. In A 28, A 29, A 30, A 31, A 48 and A 49 the trees were so far apart that they may be termed "parkland". A 27 differed from the rest of the Highland woods in being a closed plantation with bare trunks. Secondary growth of young pine and juniper was common and well grown in the woods marked + but was absent from those marked −. The undergrowth was mainly thick heather (*Calluna vulgaris* and *Erica cinerea*) and whortleberry (*Vaccinium myrtillus*).

Of the other pine woods, those marked B were closely planted young plantations of 10–20 years old, the essential feature being that the branches still grow down to near the base of the trees. There were no nesting holes and no true secondary growth, but these low branches of the trees are equivalent to secondary growth.

The remaining woods were typical older pine plantations, the trees close together (though thinned out as compared with the B woods), the canopy closed, high and shallow, the trees still so young that nesting holes were very

Phot. 1. Typical young pine plantation before side branches are cut. Dense growth. No other plants. (A 12 of Appendix.)

Phot. 2. Typical Highland pine forest. Trees well spaced, with well developed side branches, good secondary growth of juniper and sapling pine. (A 6 of Appendix.)

Face page 58

scarce or absent (pines are usually felled much earlier than broad-leaved trees). Typically, there was no secondary growth or ground vegetation, the ground being covered with pine needles. Of the woods containing secondary growth, A 34 had young pines; A 1 birch and young pine; A 4, A 5 and A 17 deciduous secondary growth; A 2 and A 3 holly; and A 10 *Rhododendron*.

For Table 4 two other woods were assessed with the Scots pine woods as they were similar in type. B 1 was Corsican pine (*Pinus nigra Poiretiana*) and contained some deciduous secondary growth; C 1 was a mixed pine and larch plantation.

Table 4 shows that five species breed almost exclusively in coniferous woods:

Siskin	Crested tit
Crossbill	Capercaillie
Goldcrest	

Of these the capercaillie very occasionally nests in pure birch and in pure oak woods; the siskin has bred in alder or birch woods—its winter haunt (also exceptionally in garden trees in the south of England); and the crested tit occasionally breeds in a birch or alder stump, but almost always only in or close to conifer woods. The goldcrest nests regularly, though very sparsely, in pure broad-leaved woods, usually in ivy. In addition to these five species, the blackcock breeds almost exclusively in pine and birch, and the coal tit nests much more numerously in coniferous than broad-leaved woods, though regular and fairly common in the latter. The long-eared owl (as shown by experienced observers' field data, not by Table 4) nests predominantly in pine trees, but is also regular in broad-leaved trees; and one parkland species, the hobby, breeds predominantly but not exclusively in isolated conifers. (From Table 4 the redstart would appear to be commoner in coniferous than broad-leaved woods, but this is not really so. It is a local species and many of the counts of broad-leaved woods were taken outside its range. P 6 (see Appendix) shows how common it can be in broad-leaved woodland—the presence of yews in this wood does not affect it). The species typically absent from and scarce in coniferous woods have already been noted.

The natural pine forests, now surviving in only a few parts of the Highlands (notably the Spey Valley), with their mature trees, open growth and rich secondary growth of young pines and juniper, present such very different conditions from the closely planted pine woods of the rest of Britain that they have been tabulated separately from the rest in Table 4, in which their respective bird populations may be seen. A number of differences depend on the geographical distributions of the species concerned and not on the habitats, northern forms such as hooded crow, siskin, crested tit and capercaillie being recorded only in the Highland forests—also the black grouse, formerly regular but now exterminated in much of England—and southern forms such as the jay, many of the warblers and the green woodpecker being scarce or absent in

the Highlands. If there were mature pine forest in the south of England, it is possible that some of the southern species found in Britain almost exclusively in broad-leaved woods would be commoner in pine woods than at present.

The typical fairly old pine plantation of England is devoid of secondary growth, and hence the species typical of secondary growth are scarce or absent. But many of these species do not avoid pine woods as such; a number of them, notably whitethroat, willow warbler, song thrush, robin, dunnock and wren, occur commonly in pure young pine plantations before the bottom branches disappear. (For further details concerning the fauna of young plantations see Lack (**5**), Schiermann (**12**) and the woods marked B in the tabulated counts in the Appendix.)

Of the predominantly coniferous species, the crossbill feeds almost exclusively on pine cones, the capercaillie (especially in winter) on pine shoots. The other species are more varied in their food, and it is difficult to associate their predominance in conifers with any particular habits or adaptations, except that the goldcrest is clearly restricted (though not absolutely) by its nesting site, since it is common in broad-leaved woods provided there is one coniferous tree in which to nest, but when conifers are quite absent it is scarce (see later discussion).

(*f*) *Larch woods*

Larch (*Larix europaeus*) woods are not very common in England, and only a few were investigated. These were closed, fairly young plantations with a high canopy, usually deeper than in Scots pine plantations. Broad-leaved secondary growth was present in those marked +. Typically, undergrowth and nesting holes were absent.

The avifauna of larch plantations closely resembles that of pine plantations, but some of the species characteristic of broad-leaved woods and rare or absent in pine woods seemed appreciably commoner in larch, notably great, blue and marsh tits, and perhaps song thrush, also jay. It should, however, be emphasized that the number of larch woods counted is too small for safe generalizations. (Some of the most characteristic pine-wood species—crossbill, siskin, crested tit and capercaillie—were not recorded from larch woods in the present enquiry; but no Highland larch woods were counted. The Scottish crossbill breeds regularly in larch and the siskin occasionally (F. C. R. Jourdain).

(*g*) *Other coniferous woods*

A few other coniferous woods (see Appendix) were counted, but too few for any generalizations concerning their bird life. The three spruce (*Picea*) plantations were very similar to Scots pine, but the canopy was denser and deeper; E 1 had secondary growth of birch, rowan (*Pyrus aucuparia*) and *Rhododendron*. The juniper and the yew woods were on chalk grassland, the trees up to 10 ft. in height, in some parts dense, in others open. The juniper

wood is similar to a young pine plantation; the yew wood has numerous holes—hence the abundance of tits and robins. G1 was a very mixed conifer plantation, chiefly of young trees.

(*h*) *Mixed broad-leaved and coniferous woods*

P 1 was mixed pine, birch, oak and holly with a little deciduous secondary growth; P 2 was a coppice with oak predominating, but with many other deciduous trees and some pine, a little secondary growth and much ivy; P 3 was a park, the trees, spaced at intervals, chiefly consisting of mature oak, with some other deciduous trees and with a few pine and spruce, locally a little secondary growth. P 4 and P 5 were closely planted, with no secondary growth, the former mainly Scots pine with some oak, the latter mainly beech with some Scots pine.

Counts were done in a few mixed woods. As can be seen, mixed woods may have a richer avifauna than any other British woods. This is to be expected, since they can provide all possible combinations of requirements. P 4 and P 5 show the effects of absence of secondary growth. P 3 was included to show the birds characteristic of a country park. P 6 is a typical broad-leaved wood, except for the presence of yews, which bring in the goldcrest. The yew was presumably present in the natural oak forests of England.

9. WINTER DISTRIBUTIONS

Winter counts were taken between November and February. The habitat distributions of the different species in the various types of woods are mostly similar to those of the breeding season. In this section the more important differences as compared with summer distributions will be mentioned.

Since this paper is not primarily concerned with geographical distributions, the disappearance of a number of migratory woodland species from Britain (which is apparent from Table 4) need have no more than passing mention. A number of other birds, such as the Turdidae, are partial migrants. Three winter visitors to Britain frequent woods: the brambling being the commonest, the redwing being regular for roosting but feeding chiefly in the open country, and the fieldfare, which is, like the redwing, characteristic of fields and hedgerows, occurring at times.

In winter, the hole-nesting species and those which require tall song posts are no longer dependent on these features, and hence are more widely distributed than in summer. The appearance of tits and woodpeckers in winter in young plantations, where they cannot breed in summer owing to the absence of nesting holes, may be specially noted. Also secondary growth, especially if deciduous, is a much less important factor in distribution than in summer.

All species of tits, with the goldcrest, nuthatch, tree creeper and an occa-

sional great and lesser spotted woodpecker, tend to form into mixed foraging parties which wander through the woods. They make their way from one wood to another along hedgerows, through gardens, etc., rarely taking long flights in the open. Hence such species are rare in extremely isolated woods, such as Wistman's Wood (H 40) on Dartmoor, which is well over a mile from any other cover. Another mixed group which often feed together in winter are the lesser redpoll, siskin, goldfinch and the tits of the genus *Parus*, this group being characteristic of birch and alder woods. Unlike the members of the first group, redpoll, siskin and goldfinch will take big flights across the open. The goldfinch was excluded as a true woodland bird and placed in Table 1, as it is much more characteristic of open country than woods when breeding; in winter, however, it is regular in woods of all types, the same applying to the greenfinch.

The roosting place is a very important factor in winter distributions, but, as already noted, it was not studied in the present paper. It may be noted that quite a number of species which feed primarily in the open country frequent woods in winter for roosting. This subject forms a wide gap in present knowledge of the bird ecology of woodlands.

As is apparent from Table 4, the most marked differences in habitat distribution between winter and the breeding season are as follows:

(1) The siskin, which breeds almost exclusively in conifers, is in midwinter found almost exclusively in birch and alder. (In the early spring it again returns to larch and pine.)

(2) Most chaffinches leave the coniferous woods, the birch, and to a rather less extent the oak woods. They form huge flocks feeding in beech woods on the beech mast, and many others frequent the open country.

(3) The brambling, which breeds in the Scandinavian birch and pine woods, visits Britain in winter. In midwinter in woods it is almost confined to beech woods, joining the chaffinch flocks in feeding on the beech mast, but it is very occasional in other woodland types, and is regular in open country. (In early spring it frequents birch and pine.)

(4) The goldcrest, while still very abundant in conifers, is quite regular in smaller numbers in oak, mixed broad-leaved and birch woods.

(5) A number of species such as carrion and hooded crows, rook, jackdaw and starling, which occur in woods in the breeding season primarily because of nesting sites, tend to leave the woods in winter for the open country, though they often return to the woods in the evenings for roosting,—rook, jackdaw, starling (and also ring dove) roosting in large flocks.

(6) Many mistle and song thrushes leave the woods for the open country after the disappearance of the autumn berries.

(7) The long-tailed tit, which in the breeding season is found mainly in secondary growth, in winter wanders through all types of woods much more commonly, and is regular in the canopy.

(8) Nearly all birds wander from wood to wood much more in winter than

in summer, hence there is a much greater tendency for species which occur almost exclusively in one type of wood to straggle into another, e.g. lesser redpolls occasionally occur in all the main types of woods, though typical of birch only (also pine in early spring); and the nuthatch, which is typically confined to broad-leaved woods, is very occasional in pure conifers.

10. DISTRIBUTIONS AT OTHER SEASONS

Distributions of woodland birds at seasons other than the breeding season and midwinter were not studied in this enquiry, so only a few brief and incomplete notes are given here. It should be specially noted that the change-over from the breeding to the winter type of distribution occurs in many species immediately after they have nested, in the middle of the summer, and in some cases before other species of woodland birds have finished breeding. Thus already in late June some of the tit and goldcrest parties have formed and wander into habitats not frequented in the spring, and in late summer and early autumn a number of the warblers and the spotted flycatcher join up with these foraging parties, feeding on the insects disturbed by the tits.

When caterpillars, notably of *Tortrix*, swarm in late summer, there is an influx of many species to the woods to feed on them, including rook, starling and many smaller birds. The rowan and other autumn berries bring an influx into the woods of various species, particularly the Turdidae, including the ring ouzel, a passage migrant from the moors. Ring doves are common in oak woods when the acorns fall, and also invade the Dartmoor oak woods when the whortleberries (*Vaccinium myrtillus*) ripen. In the early spring some of the winter visitors from the north, notably brambling, lesser redpoll and siskin, move from their winter to their summer habitat, as noted in the last section. Some movement goes on among woodland birds even in the middle of the breeding season, for the pure oak coppice woods on the edge of Dartmoor are almost devoid of birds until the leaves appear in mid-May, after which there is a marked influx of chaffinch, robin, wood warbler and a few other species (Lack). In both spring and autumn, migrant birds on passage stop for a while in woods of types sometimes unfrequented by them at other seasons, but these occurrences are not of sufficient ecological importance for detailed reference.

The above notes are extremely incomplete, but are sufficient to show that the bird population of woods is far from static at any season.

11. COMPARISON WITH THE NORTH EUROPEAN MAINLAND

Palmgren (**9**, **10**, **11**) has made most valuable and detailed studies of habitat distribution in the woods of south Finland, and when similar studies have been made in the rest of Europe, some very interesting comparisons

will emerge. Schiermann (**12**) gives habitat data from north Germany and Sundström (**14**) from Finland; but for the rest of Europe the data are almost confined to general avifaunal studies, notably by Niethammer (**8**).

Comparison with Palmgren's data in particular shows many striking similarities in the habitat distributions of the various woodland species, even when these refer to different geographical subspecies. For instance, in south Finland great and blue tits (different subspecies from the British races) are mainly in broad-leaved woods, but regular, though very uncommon, in pure coniferous woods—just as they are in Britain. There is no need to comment specially on the many other points of similarity. The large number of British woodland birds which are represented by different subspecies from the Continental forms indicates that the British woodland avifauna has been isolated from that of the Continent for a long time, but nevertheless the habitat distributions have remained nearly the same.

As regards the differences in distribution between south Finland and Britain some, such as the predominance in south Finland of jay, bullfinch, mistle thrush, song thrush, robin, wren and ring dove in coniferous woods (some in spruce, some in pine) as opposed to broad-leaved woods, are perhaps not correlated directly with the species of trees, but with other local conditions, since these birds show no such tendency in Britain, where a much greater variety of broad-leaved woodland types are afforded than Palmgren could investigate in south Finland. Some further differences are detailed below.

Tree creeper: Palmgren notes *Certhia f. familiaris* (L.) as restricted to conifers. Stresemann (**13**) in a general survey states that this is true of much of its range, but that in parts of its European range it occurs in broad-leaved woods. The British race, *C. f. brittanica* Ridgw., seems quite as common in broad-leaved as coniferous woods. Incidentally the American form (*C. f. americana* Bp.) is by no means restricted to conifers.

Goldcrest: Palmgren notes *Regulus r. regulus* (L.) as confined to conifers, and this is supported by other Continental authorities. In Britain it is a sparse, but quite regular, breeding species in pure broad-leaved woods, and is quite common there in winter.

Coal tit: Parus a. ater L. would also seem to be nearly confined to conifers, though not entirely. The British race is common in broad-leaved woods, though not so abundant as in conifers.

Willow tit: Parus atricapillus borealis Selys-Longchamps, is regular in south Finland, not only in broad-leaved woods, but also in pure coniferous woods, a habitat in which the British race was not recorded breeding unless a birch or alder stump was present.

Chiffchaff: Schiermann records *Phylloscopus c. collybita* (Vieill.) as regular in pine plantations, and in south Finland Palmgren records *P. c. abietinus* (Nilss.) as true to spruce. In the present British enquiry, almost no chiffchaffs were recorded from pure coniferous woods.

Lesser whitethroat: Both Palmgren and Schiermann record this bird as typical of coniferous scrub, whereas in England it is almost always in broad-leaved deciduous scrub.

12. HISTORICAL CONSIDERATIONS

Any consideration of present habitat distributions must eventually take into account the distributions in the past, though knowledge of the latter is necessarily speculative. It seems probable that after the last Glacial Period there was a period when even the south of Britain was covered with conifer and birch forest, which presumably contained only the birds characteristic of these woods, such as crossbill, siskin, lesser redpoll, tree creeper, goldcrest, coal tit, willow tit, crested tit, capercaillie and black grouse. Gradually the conifer-birch belt must have moved northwards, to be replaced in the south by mixed oak forest, and with this change some of the more southern birds characteristic of oak woodland, such as marsh tit, nuthatch, nightingale, lesser spotted woodpecker and green woodpecker—presumably colonized the country. At the same time, many of the birds of the conifer-birch forest presumably retreated northwards, amongst them crested tit, siskin and Scottish crossbill. But other species, especially the tree creeper and coal tit, and to a less extent the goldcrest, would seem to have spread into the oak woodland with success. As regards the goldcrest, it breeds only sparsely, though regularly, in pure oak woods, but it was probably much commoner in the natural oak forests of England than this suggests, for it readily breeds in isolated yew trees even when all the other trees are broad-leaved. For instance, it is common in the New Forest in woods containing purely broad-leaved trees except for yews (P 6 in the Appendix is a typical population for this type of woodland). Yews were presumably present in the natural oak forest. Hence the goldcrest has adapted itself less than tree creeper or coal tit, but sufficiently for it to be regular in natural oak forest.

In addition to these natural changes in the forest conditions, man has caused drastic changes. Except for some natural pine forest in the Scottish Highlands, almost no extensive original forest survives in Britain to-day. Planted woodlands cover a far smaller area than the original forests did, hence possibly the Corvidae and some other birds were once much less frequent outside woods than they are to-day. Further, the conditions in a planted wood are different from those of natural forest. Oak and mixed broad-leaved planted woods are often permitted to grow for so long that they simulate small areas of natural broad-leaved forest (except with regard to the frequent absence of yews, which affects the goldcrest); but coniferous plantations are usually cut long before they approach the conditions of natural forest. Plantations are usually closely planted and have little or no secondary growth, and are often

so young that nesting holes are absent. Hence they afford much less suitable conditions than does natural forest for many woodland birds.

Man has further upset the natural conditions by introducing types of trees not naturally found in the area concerned. Various species of trees foreign to Britain have been introduced, most only as isolated trees, but some, and in particular the larch, in extensive plantations. Of particular interest, especially during the last hundred years, Scots pine has been reintroduced on a large scale in much of southern and eastern England. It is interesting to compare the birds of these new southern pinewood areas with those of the natural pine forest in Scotland, the latter presumably resembling the avifauna of southern England at an earlier time. As might be expected, the three characteristic coniferous species which have successfully colonized the southern oak woodland, namely coal tit, tree creeper and goldcrest, have colonized these new pinewood areas. (The present scarcity of the tree creeper can be correlated with the scarcity of old trees suitable for its nesting cracks in the new plantations.) But the other coniferous species, such as siskin and crested tit, now restricted to the north of Britain, have failed to colonize. It is of special interest that, although another member of this latter group, the Scottish crossbill, has also failed to colonize, the Continental race of this bird (*L. c. curvirostra* L.), which periodically irrupts into England, has now established itself in these southern pinewood areas.

13. Factors influencing habitat distribution

A species may be limited in its habitat distribution by various factors: food (e.g. crossbill), feeding habit (flycatchers), song post (blackcap), nesting site (hole-nesters), nest material (nightingale), and roosting place (pheasant). Further examples of these types will be found in the text, and Palmgren (**10**) may be referred to for admirable examples, worked out in detail, of nesting restrictions. It should be emphasized that though these habits are *associated* with the limitations concerned, it does not follow that they are the *cause* of the limitations. In many other cases, the limitations cannot be correlated with any known habits or adaptations, and though in some cases this may be due to the inadequacy of present knowledge, it seems probable that in many cases such associated habits and adaptations do not exist.

A further difficulty in accounting for the restrictions of certain birds to woods of a particular kind of tree is that, in nearly all such cases, the bird does occasionally breed in other wood types. For instance, both goldcrest and capercaillie, typically confined to conifers, occasionally breed in oak woods, and the nightingale, typical of broad-leaved woods, has bred in pure conifers. Other examples were given earlier. In other cases the species is typical of one wood type, but is regular in very much smaller numbers in another type; for instance blue and great tits are typical of broad-leaved woods, but regular,

though much less common, in pine woods. There is a gradation through species like the coal tit, which to judge from its frequency index is rather more than twice as common in conifers as in broad-leaved woods for breeding, to species like the chaffinch which is almost equally common in all types of woods.

The distribution of the black grouse, which is regular in both pine and birch, but not in other broad-leaved types, is particularly difficult to understand, since no environmental factor common to pine and birch, but lacking in the other broad-leaved types, is apparent in a study of either the woods concerned or of the habits of this bird. Another interesting point is that the British tree creeper and British coal tit seem to breed much more frequently in broad-leaved woods than do the Continental subspecies of these birds.

In their inability to interpret most of the observed habitat restrictions and limitations to distribution, the writers find themselves in much the same position as Lack (**4**) on the Breckland, and Moreau (**7**) in the Usambara forests. It seems that, while some limitations are correlated directly with particular environmental factors or with structural adaptations, these cannot account for all cases, and that habitat selection is determined in part by factors on a psychological plane, the significance of which is connected with the past history of the species. (Some general aspects of the psychological factor in habitat selection are discussed by Lack (**6**); the following discussion should be considered an addition to this review.)

It may be tentatively suggested that the greater frequency in broad-leaved woods of the British tree creeper, coal tit and goldcrest than the Continental subspecies of these same birds, may be due to a psychological rather than a structural adaptation. (If any structural adaptation is present it must be extremely inconspicuous.) Again, it may be a limitation of habit rather than of structure which restricts the black grouse to pine and birch, perhaps because of this species being originally a northern bird for which the only available wood types would be conifers and birch. The latter habitats may be instinctively selected, while the other broad-leaved wood types are not, although the latter (due especially to human planting) are now within the black grouse's geographical range and are perhaps not otherwise unsuitable.

One of the most puzzling features of British woodland bird distributions is this restriction of certain species to conifer, to birch or to oak broad-leaved woods. As already noted, these restrictions could not, in most instances at least, be correlated with any structural adaptations or particular habits. In many cases, however, they can be correlated with one factor, namely geographical distribution. Of the eight species classified as typical of pine or birch, seven (siskin, lesser redpoll, Scottish crossbill, crested tit, willow tit, capercaillie and black grouse, i.e. all save goldcrest) are predominantly, and some exclusively, northern birds in Britain to-day. On the other hand, of the ten species typical of oak-woodland six (hawfinch, nuthatch, marsh tit, chiffchaff, nightingale and lesser spotted woodpecker) have definitely southern

distributions (possibly blackcap, garden warbler and wood warbler could be added), and so has the green woodpecker (from the list of four additional predominantly broad-leaved woodland species).

This correlation is far too striking to be due to chance, and with the apparent absence of other correlated factors we may seek in geographical distributions for an explanation of the habitat restrictions. What is the significance of the correlation? Certainly the limit to the geographical distributions of the birds is not caused by adherence to a type of tree which is geographically restricted. Thus nuthatch, marsh tit, nightingale and the rest disappear towards the north long before broad-leaved woodland becomes scarce. Similarly, siskin, crested tit, etc., disappear or become scarce in the south where coniferous plantations are common. On present evidence, the most probable explanation seems to be along the lines already suggested for the black grouse that a number of southern species (not, of course, all) tend to frequent oak broad-leaved woodland, and a number of northern species tend to frequent pine and/or birch, simply because these were the habitats originally available to the species in question, and the inherited habits of these species are now such that they tend to select the ancestral habitat even when, as in Britain to-day, other habitats, quite possibly suitable, have become available.

A further characteristic of these habitat restrictions is that an exceptional break-away from the restriction has been recorded in Britain for nearly every species concerned, and for the remainder on the European mainland; the existence of such exceptions is much easier to account for if the restrictions are primarily due to habit and not to structural adaptation. It is not intended to rule out the possibility of structural adaptations being involved in some cases, though if such exist it seems quite probable that the structural adaptation was evolved subsequently to the habit; however, it may be pointed out that adaptive structural differences are more characteristic as between different genera of birds than as between different species of the same genus, and in the distributions under discussion one may find only one species out of several in the genus showing the restriction in question (cf. tits), or even only some, and not all, of the subspecies of one species (cf. goldcrest, chiffchaff). The general considerations of the nature of bird behaviour which make such restrictions of habit, and so of habitat, not only possible, but likely, have already been discussed by Lack (**6**).

14. The woodland bird community

In previous sections the niches in woods filled by the various woodland birds have been described and to some extent discussed. The interrelations of woodland species cannot be adequately described without quantitative study, which was not an object of the present enquiry, but a few points may be briefly mentioned.

There is competition for nesting holes among certain species, but in most

species competition for nesting sites is entirely absent. Some species, e.g. hobby, tend to use the nests of other species. Various species eat the same sorts of food, but there is no definite evidence as yet as to whether, and to what extent, one species significantly affects another as a result of this. A few species of birds prey on the adults, or eggs and young, of others. Territorial behaviour perhaps affects the density of individuals within a species, but there is very little evidence of one territorial species thereby affecting the density of another. The foraging parties outside the breeding season perhaps result in mutual benefit, one species disturbing insects which are thus rendered available for another. In these and other ways, the various woodland species interact, but the general impression gained is that the woodland bird "community" is extremely loosely knit: most of the species are by no means confined to woods, many seem quite independent of any other bird species, and in many others the interaction is extremely slight—from the standpoint of population density perhaps negligible. The various woodland birds occur in woods correlated with widely different features in different cases. Vegetational factors, and not other bird species, are primarily responsible for their occurrence side by side, and the birds interact with each other to a far smaller extent than the members of a plant community.

15. SUMMARY

1. A co-operative survey was organized under the auspices of the British Trust for Ornithology, in the course of which 152 woods were investigated in summer and 120 in winter. Fifty-seven individuals and organizations took part in the survey.

2. The requirements of British woodland birds are summarized in Tables 1–3, and a comparative index of their abundance in different types of wood is given in Table 4. The full data are contained in an Appendix.

3. Some species are limited to open as opposed to close woods, others are limited by secondary growth, nesting holes, tall trees (as nests or song posts), and a few by water.

4. Both mixed broad-leaved woods and natural pine forest are rich in birds, but plantations of both are poor, correlated with close planting and scarcity of holes and secondary growth.

5. Eleven species of birds are almost confined to broad-leaved as opposed to coniferous woods (two of these being characteristic of birch), and five to coniferous as opposed to broad-leaved woods. A few species are abundant in all the main types of woods.

6. The winter habitat distributions are mainly similar to those of the breeding season, the exceptions being discussed.

7. Comparison with the north European mainland shows that most habitat distributions and limitations are the same, with some exceptions that are mentioned.

8. Some habitat limitations can be associated with particular habits or adaptations, but this does not necessarily mean that the latter are responsible for the limitations. For the most part, such associated habits or adaptations have not been found. But the restriction of certain species to conifers or birch or both, and of others to oak woodland could definitely be correlated with geographical distribution, the former being mainly northern and the latter southern species. It is tentatively suggested that this is correlated primarily with habitat limitations on a psychological plane associated with the past history of the species.

REFERENCES

1. **Collinge, W. E. (1927).** "The food of some British wild birds." York.
2. **Elton, C. (1935).** "A reconnaissance of woodland bird communities in England and Wales." J. Anim. Ecol. 4: 127–36.
3. **Jourdain, F. C. R. (1920).** Food summaries in "A practical handbook of British birds", ed. H. F. Witherby. London.
4. **Lack, D. (1933).** "Habitat selection in birds: with special reference to the effects of afforestation on the Breckland avifauna." J. Anim. Ecol. 2: 239–62.
5. **Lack, D. (1937).** "A review of bird census work and bird population problems." Ibis: 369–95.
6. **Lack, D. (1937).** "The psychological factor in bird distribution." Brit. Birds, 31: 130–6.
7. **Moreau, R. E. (1934).** "A contribution to tropical African bird-ecology." J. Anim. Ecol. 3: 41–69.

7*a*. **Moreau, R. E. (1935).** "A critical analysis of the distribution of birds in a tropical African area." J. Anim. Ecol. 4: 167–91.

8. **Niethammer, G. and others (1937).** "Handbuch der deutschen Vogelkunde." Vol. 1. Leipzig.
9. **Palmgren, P. (1930).** "Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands, mit besonderer Berücksichtigung Ålands." Acta Zool. Fenn. 7: 1–218.
10. **Palmgren, P.(1932).** "Zur nistökologischen Analyse dreier Waldvogelarten, *Fringilla coelebs* L., *Regulus regulus* (L.) und *Carduelis spinus* (L.)." Ornis Fenn. 11: 33–7.
11. **Palmgren, P. (1930).** "Zur Biologie von *Regulus r. regulus* (L.) und *Parus atricapillus borealis* Selys...." Acta Zool. Fenn. 14: 1–113.
12. **Schiermann, G. (1934).** "Studien über Siedelungsdichte im Brutgebiet. 2. Der brandenburgische Kiefernwald." J. Orn. (Leipzig) 82: 137–86.
13. **Stresemann, E. (1919).** "Über die europaischen Baumlaufer." Verh. Orn. Ges. Bayern, 14: 39–74.
14. **Sundström, K. E. (1927).** "Ökologisch-geographische Studien über die Vogelfauna der Gegend von Ekenäs." Acta Zool. Fenn. 3: 1–170.
15. **Venables, L. S. V. (1937).** "Bird distribution on Surrey Greensand heaths: the avifaunal-botanical correlation." J. Anim. Ecol. 6: 73–85.

APPENDIX

COMPLETE TABULATED COUNTS FROM SURVEYS

(1) *District*. The following abbreviations are used:

S.E. South-east England (Kent, Sussex, Surrey, Hampshire).
S.W. South-west England (Dorset, Devon).
C. Home Counties (Middlesex, Hertfordshire, Oxfordshire, Berkshire, Buckinghamshire).
E. Eastern England (Cambridgeshire, Suffolk, Norfolk).
M. Midlands (Nottinghamshire, Cheshire, Shropshire, Worcestershire).
N. Northern England (Yorkshire, Lancashire, Cumberland, Westmoreland).
Sc. Scotland excluding Highlands (Midlothian, Perthshire, Dumbartonshire).
H. Highlands of Scotland (Inverness-shire).

(2) *Secondary growth.*

+ indicates present in fair quantity.
½ indicates present but very sparse.
– absent, or almost entirely absent.

(3) *Number of counts*. Where more than one count was taken, the figures indicate the largest number of individuals of the species seen on any one walk.

(4) *Reference numbers*. These correspond with those on the detailed woodland descriptions deposited with the British Trust for Ornithology.

A NOTE ON THE FOOD OF PIKE (*ESOX LUCIUS*) IN WINDERMERE

By K. R. ALLEN

Assistant Naturalist at the Laboratory of the Freshwater Biological Association, Wray Castle, Ambleside, Westmorland

THIS paper is based on the examination of the stomach contents of 103 pike captured in Windermere between August 1933 and October 1935. The majority of the fish caught were taken in a seine net worked on the shores of the lake, but a few were obtained by angling. The results of the examination of a few pike netted in Rydal Water are also included in this paper, since conditions in this lake are similar in many respects to those in Windermere.

The food of pike consists principally of small fish, and this has been found to be the case in Windermere. A few of the pike had also been feeding to some extent upon invertebrate animals. Four species of fish were found in the stomachs: perch (*Perca fluviatilis*), trout (*Salmo trutta*), minnow (*Phoxinus phoxinus*), and three-spined stickleback (*Gasterosteus aculeatus*). These include all the fish common in the lake except the char (*Salvelinus willughbii*), eel (*Anguilla vulgaris*), and the pike itself. The char lives during the greater part of the year in the open water away from the shore, and only comes into shallow water when spawning. Since the pike appears to be largely confined to the littoral region of the lake, the char is therefore hardly available to it as food. But as all the pike referred to in this paper were caught near the shore, no evidence is available as to whether the few pike living in deep water feed on the char. The burrowing and bottom-living habits of the eel make it somewhat inconspicuous and therefore less available to the pike. The absence of small pike from the food of the larger ones is rather striking.

The net used for catching pike had a mesh of 2·5 cm. knot to knot, and therefore allowed pike under about 30 cm. in length to escape. The large baits used when angling for pike rarely attract fish under about this size. Consequently the sample of pike collected consisted almost entirely of fish over 30 cm. (see Table 1, which shows the size distribution of the pike caught). It is probable that this table gives a fairly accurate representation of the size distribution among the larger pike in the lake.

A comparison has been made between the stomach contents and the size of the pike, but there is no suggestion of any change in the species eaten as the pike grow larger. This, of course, does not suggest that there is no change of this nature in pike less than 30 cm. in length; and in fact it is obvious that

at one stage at least in the growth of the pike there must be a change in the type of food eaten. Balfour-Browne (1907) found that in Sutton Broad the first food of young pike fry was Entomostraca, including fairly large Daphnids.

Table 2 shows the number of pike containing each of the principal types of food. The perch is clearly the most important food. When it is considered that probably a great proportion of the fish which were too far digested to be identified were also perch, the predominance of the perch over all other foods

Table 1. *Size distribution of pike caught*

Length ... in cm.	15·0–19·9	20·0–24·9	25·0–29·9	30·0–34·9	35·0–39·9	40·0–44·9	45·0–49·9	50·0–54·9	55·0–59·9
No. of fish	1	—	2	13	15	20	12	10	11
Percentage of catch	1	—	2	12	14	19	12	10	11

Length ... in cm.	60·0–64·9	65·0–69·9	70·0–74·9	75·0–79·9	80·0–84·9	85·0–89·9	90·0–94·4	95·0–99·9	Total
No. of fish	9	6	1	—	1	1	—	1	103
Percentage of catch	9	6	1	—	1	1	—	1	100

Table 2. *The number of pike found to contain each food animal*

Food	No. of fish
Ephemera danica nymphs	6
Leptocerus larvae	1
Earthworms	1
Total with invertebrates	7
Phoxinus phoxinus	9
Gasterosteus aculeatus	8
Perca fluviatalis	42
Salmo trutta	2
Unidentifiable fish	18
Total with fish	68
Empty	32

becomes even greater. The relative numbers of perch and trout eaten by the pike correspond very approximately to their actual numbers in the lake, and it might appear that the pike showed no well-marked preference for either species. In winter, however, the perch are all in water about 20 m. deep and are practically absent from the littoral region. This is shown by the fact that during the months November to March seine netting yielded 288 trout and only two perch. Despite this the pike captured during these months contained four perch and only one trout. Thus it appears that the perch is either very much more easily caught than the trout, or else is definitely selected by the pike.

The two species of small fish eaten by the pike, the minnow and the three-spined stickleback, were eaten in approximately equal numbers. The minnow is, however, very much more abundant than the stickleback in the lake, and occurs in very large shoals. Since it has also been shown that perch which were feeding on fish contained minnows only slightly more frequently than sticklebacks (Allen, 1935), it appears likely that owing to some difference in

habit or habitat the stickleback may be rather more available to carnivorous fish than is the minnow.

Table 2 shows that the only invertebrate animal frequently eaten by the pike is the nymph of a mayfly, *Ephemera danica*. All the pike which had been eating these were caught in June, and had been taking mature nymphs, apparently as they rose to the surface preparatory to hatching.

It is clear that it is to the advantage of a fish to change its diet as it increases in size so as to increase correspondingly the size of the food particles. This frequently leads to changes in the actual type of food taken, as has been shown to occur in the perch (Allen, 1935). Pike in the size range considered in this paper do not show a change of this nature. It is also possible that among fish feeding on the same type of food the larger individuals may choose larger individual food organisms. In nearly every case where a fish was found in the stomach of a pike its length was recorded, and consequently it is possible to determine the average size of fish eaten by pike of various sizes. It was found that pike more than 38 cm. long tended to eat larger fish than did pike of less than 38 cm. The respective mean lengths of the fish eaten by these two classes of pike were 8·65 and 6·02 cm. Application of the t-test (Fisher, 1936) to these results shows that the probability of such a difference in the mean with random sampling was less than 0·01, so that this difference is evidently significant. No further differences of this type could, however, be found by subdividing these two classes of pike.

Table 2 also shows that the proportion of empty stomachs among the pike examined was very large. This high proportion of empty stomachs appears to be characteristic of fish-eating fish. Nilsson (1921) found that out of 38 pike stomachs examined 20 were empty. The significance of this phenomenon has been discussed in a previous paper (Allen, 1935), where it was shown that in the perch the change to a fish diet was accompanied by an increase in the percentage of empty stomachs. As in the perch, a greater proportion of empty stomachs is found in the pike in winter than in summer. Out of 32 pike caught in the months November to March, 14 (44 %) contained no food, while during April to October only 19 out of 71 (27 %) were empty. This increase in the proportion of empty stomachs in winter is very probably due to the reduced rate of metabolism in the fish at the lower temperature.

Summary

1. This paper gives the results of the examination of the stomach contents of 103 pike, taken chiefly from Windermere.

2. The fish examined, few of which were less than 30 cm. long, had been feeding almost entirely upon other fish, principally perch.

3. The only invertebrate food taken to any great extent was hatching nymphs of *Ephemera danica*.

4. Pike less than 38 cm. long tended to eat rather smaller fish than did larger pike.

5. The percentage of pike with empty stomachs was high at all times, but higher in winter than in summer.

REFERENCES

Allen, K. R. (1935). "The food and migration of the perch (*Perca fluviatilis*) in Windermere." J. Anim. Ecol. 4: 264–73.

Balfour-Browne, F. (1907). "On the early stages in the life histories of certain fresh-water fishes." Trans. Norfolk Norw. Nat. Soc. 8: 478–88.

Fisher, R. A. (1936). "Statistical methods for research workers." 6th ed., London.

Nilsson, D. (1921). "Några insjöfiskars ålder och tillväxt i Bottniska viken och Mälaren." Medd. LantbrStyr., Stockholm, no. 231.

A SURVEY OF THE STATUS OF *RATTUS RATTUS* AND ITS SUBSPECIES IN THE SEAPORTS OF GREAT BRITAIN AND IRELAND

By COLIN MATHESON

Department of Zoology, National Museum of Wales

(*With* 5 *Figures in the Text*)

CONTENTS

	PAGE
1. Introduction	76
2. Questionnaire	78
3. England and Wales	79
(*a*) Black rats on ships: results of fumigation	79
(*b*) Black rats on shore	84
4. Scotland and Ireland	90
5. Relative numbers of the three subspecies of *Rattus rattus*	91
6. Summary	93
References	93

1. Introduction

The history of *Rattus rattus* and of *R. norvegicus* in this country is familiar to most zoologists, and only a few words need be said on the subject here. The black rat (*R. rattus*) is believed to be an alien which first reached our shores some time in the Middle Ages, a common suggestion being that it was brought back from the east on the ships of the Crusaders; at any rate it was an established and numerous member of our fauna for several hundred years, and the only species of rat existing in Britain. The brown rat (*R. norvegicus*) is an alien which is known to have appeared for the first time in Britain about the beginning of the eighteenth century. (Regarding the reported occurrence of bones of *R. norvegicus* in deposits at Kilgreany Cave, Ireland (**5**), Dr Wilfrid Jackson has written to me: "The upper levels were loose and somewhat disturbed, and I think the brown rat is a fairly recent intrusion there.") This is a larger animal than the black rat and more adaptable generally, and there seems little doubt that it was responsible for the complete disappearance of the latter from most parts of the British Isles.

In many districts the black rat had been driven out before the end of the eighteenth century, though it survived, in dwindling numbers, in some inland places till about the middle of the nineteenth or later (**6**). During the latter

part of the nineteenth century it seems to have disappeared entirely, except in a few islands and some of the seaports on the mainland. Whether it ever became quite so scarce at these ports as is often stated, may be doubted. The following extract from an article in *Notes and Queries* of 1854 (10: 335) is suggestive: "In 1845...there was an intelligent man, and not a bad naturalist for his station in life, who exhibited a "Happy Family" opposite the National Gallery. He generally had three or four black rats in his cage....He informed me that he had long known that the black rat inhabited the upper parts of the old houses in St Giles's; and that when applied to by naturalists for a specimen of the animal, he took care to represent its exceeding rarity, though by setting traps in these houses he could catch one almost whenever he pleased. He also stated that his usual price for a specimen used to be three guineas." At Great Yarmouth there was a colony which was the subject of a series of notes from 1896 onwards (**7**, **8**).

In later years, the species was found to exist in some numbers at various ports, and the usual assumption appears to have been that these numbers were kept up by specimens escaping from ships. For example, with regard to the Yarmouth colony, Patterson, as quoted by Hinton (**4**), wrote in April 1918, that they were now "becoming rarer....The war allows no grain ships here, so that the species does not now breed ahead of its destruction." *R. rattus* is, it may be noted, by far the commoner species on ocean-going vessels, the brown rat being usually entirely absent. Thus, of the total number of rats destroyed on ships in Cardiff Docks by the rat-catcher during the years 1922–8 inclusive, 22,036 were black rats and only 50 were brown; at Liverpool, from 1929 to 1937 inclusive, 28,956 ship rats were of the black species, and only 72 were brown.

In recent years there has been a great intensification of efforts to eradicate rats on board ships. One object of the present enquiry was to illustrate the work done in this respect at British seaports and its results; but the main object was to determine, if possible, whether the decrease of black rats on ships visiting British ports had resulted in any corresponding decrease of black rats on shore—in other words, whether the black rat population on shore is dependent on immigrants from ships or can be regarded as an established part of our mammalian fauna. It will be advisable at this point briefly to outline the measures against rats adopted at all the bigger ports at the present time.

Formerly, rat-infested vessels arriving in British ports were dealt with under the powers conferred by the Rats and Mice (Destruction) Act, 1919. At Cardiff, for example, in 1926, 42 notices were served on masters of vessels under the Act; 23 vessels were fumigated (resulting in the death of 575 rats and 18 mice), and the rat-catcher carried on operations on board 55 vessels. Enquiries were made on board every vessel arriving at the port as to the presence of rats. The vessels reported to be rat-infested on arrival were examined by inspectors,

while many vessels were found on inspection to be infested, although reported rat-free on arrival.

The procedure has now been greatly modified as a result of Article 28 of the International Sanitary Convention of Paris, 1926, which recommended that the master of every vessel coming from a foreign port should have to produce a certificate issued within the last six months, at an approved port, stating either that the vessel had been deratized there (deratization certificate), or had been found on inspection to be free from rats (exemption certificate). This recommendation was widely adopted from 1928 onwards; thus at Cardiff in 1929, 181 deratization and 110 exemption certificates were issued to masters of ships. Article 28 of the Paris Convention was subsequently made compulsory by the Public Health (Deratization of Ships) Regulations, 1929, which came into effect on 1 January 1930 and are now incorporated in the Port Sanitary Regulations, 1933.

In addition to measures designed to reduce the number of rats on ships, British ports to-day adopt many precautions to prevent the passage of rats from ship to shore, or vice versa. The following summary of the methods in operation at Southampton will serve as an illustration, these methods being in essentials the same at all ports. (1) The ship must be so moored as to be at no point less than 6 ft. from the quay. (2) All warps, etc., used for mooring must be fitted with canvas rat-guards (coated daily with tar) or with shields or disks. (3) No gangways or planks connecting ship and shore are allowed except that in actual use; and the latter, if not in constant use, must have a man in attendance day and night and be provided with a light at night. (4) Booms and other appliances keeping the ship in position and connecting it with the quay must be coated with tar parcelling and the tar renewed daily.

It is, however, probable that a number of rats still get ashore: one Medical Officer of Health, in his *Annual Report*, suggests that the majority do not land "via the mooring ropes, etc., but are landed with cargo in crates, etc...." The chief object of the present enquiry was to ascertain whether the intensive methods of rat destruction on ships now in force at British ports have in fact resulted in any definite decline of the black rat population on shore. As will be clear from the preceding paragraphs, the new regulations regarding rat destruction on vessels have now been obligatory at all ports for over nine years, and were actually adopted at many ports still earlier; so sufficient data should be available to furnish a definite indication of the effects on *R. rattus* both on ships and ashore.

2. Questionnaire

With the collaboration of Dr J. Greenwood Wilson, Medical Officer of Health for the City and Port of Cardiff, a questionnaire was drafted asking for information on the following points:

(1) The numbers of black rats and of brown rats destroyed (*a*) on ships,

(*b*) on docks, quays, wharves, and in warehouses and other premises ashore, in each year from 1925 to 1937 inclusive.[1]

(2) In the case of black rats, the numbers (if available) destroyed of each subspecies—*R. rattus rattus*, *R. r. alexandrinus* and *R. r. frugivorus*.

(3) Any known factors, apart from an actual decrease or increase in the rat population, which might affect the total number of rats destroyed from year to year, e.g. whether the amount of rat-catching conducted has fluctuated or remained fairly constant over the period 1925–37.

(4) Number of ships examined for rats each year, number of ships fumigated, and number of rats found dead per ship after fumigation, during the period 1925–37.

(5) Any information available as to the ratio of male to female rats.

(6) In general, any observations of interest you may care to make on the rat situation in your port health district.

A copy of this questionnaire was sent, with a covering letter, to the Medical Officer of Health of the Port Health Area of each "approved port" in Great Britain and Ireland. With the exception of the data for Cardiff, which are largely the result of the writer's own records, the present paper is based mainly on 22 replies received to this questionnaire; though some of the replies cover too short a period, or are not sufficiently detailed, for use in the tables and graphs. To the Port Medical Officers concerned, and in particular to Dr J. Greenwood Wilson, I wish to tender my grateful thanks.

3. ENGLAND AND WALES

(*a*) *Black rats on ships: results of fumigation*

There can be little doubt that rat infestation of ships is now very much less than formerly. Fumigation of a ship in London Docks is recorded to have yielded as many as 1700 dead rats (**3**). The difference to-day is well illustrated by the following quotation (relating to all the ports in England and Wales) from the *Annual Report* for 1936 of the Chief Medical Officer of Health. "The largest number of rats recorded from any one ship as a result of fumigation was 338...it is now rare to find anything approaching this degree of infestation." At the Port of London, the average number of rats per ship found dead after fumigation has in recent years varied from about four to six. The replies sent to query 4 of the questionnaire include records of four ships at one port in 1927,

[1] The classification into black and brown is of course done by the lay staff, but the probability of any important error is small. The inspectors, etc. concerned are trained to distinguish the species; and as the great majority of ship rats are correctly recorded as black (despite the resemblance of the common subspecies *alexandrinus* to the brown) the records on shore may be taken as equally correct. Any error that did occasionally occur would lie in recording black rats (*alexandrinus* type) as brown—no brown rat (save infrequent melanic specimens) could ever be recorded as black; and such an error if corrected would obviously strengthen, instead of weakening, the conclusions drawn in this paper.

with an average of 235·5 rats per ship, and one ship at another port in 1933 with 100 rats; but at these and other ports such figures are now very uncommon.

Seven ports have supplied statistics going back to 1925, and the average number of rats found per ship after fumigation, calculated on the aggregate figures for these seven ports, was as follows for the earlier years, before the general adoption of the recommendations of the Paris Convention: 1925, 30·4 rats per ship; 1926, 23·0; 1927, 23·0; and 1928, 20·6 rats. Fig. 1, based

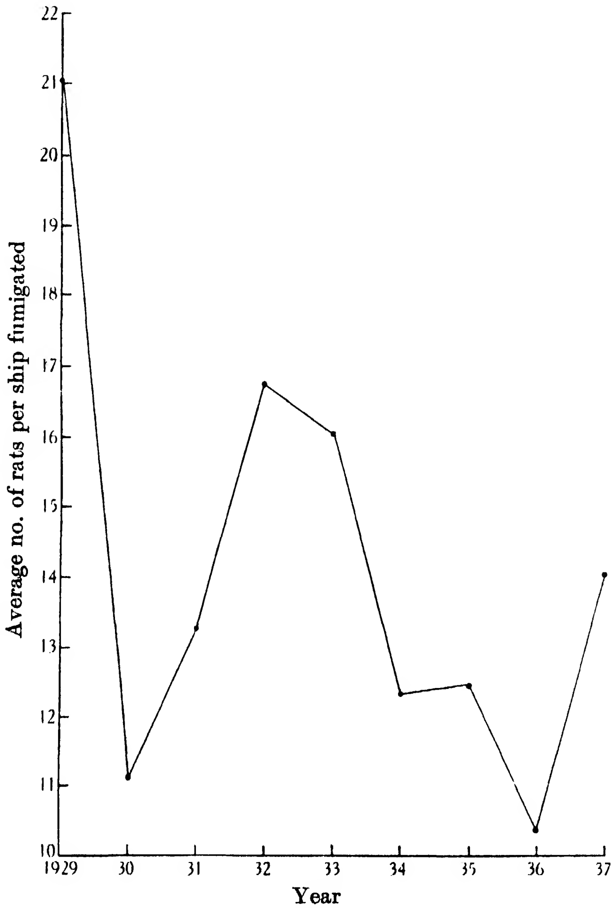


Fig. 1. Average number of rats per ship found dead after fumigation in each year from 1929 to 1937. (Based on the figures for ten seaports in England and Wales—see Table 1.)

on the statistics for ten seaports in England and Wales (Table 1), indicates the average number of rats per ship found dead after fumigation, in each year from 1929 to date. It appears that, since 1929, the average number of rats has not greatly altered, fluctuating around a figure of about 13 rats per ship. This general conclusion holds for most of the ports individually, as study of Table 1 will show; the actual figure for rats per ship varies, of course, from port to port, but the figure at each port has of late shown little decrease from year to year. (This applies also to the statistics for Hull, received too late for inclusion in the

Table 1. *Number of ships fumigated, and average number of rats per ship found dead after fumigation, at ten seaports in England and Wales, for each year from* 1929 *to* 1937

Year	R. Blyth: Ships fumigated	R. Blyth: Rats per ship	Bristol: Ships fumigated	Bristol: Rats per ship	Cardiff: Ships fumigated	Cardiff: Rats per ship	Liverpool: Ships fumigated	Liverpool: Rats per ship	Manchester: Ships fumigated	Manchester: Rats per ship	Middlesbrough: Ships fumigated	Middlesbrough: Rats per ship	Newport: Ships fumigated	Newport: Rats per ship	Southampton: Ships fumigated	Southampton: Rats per ship	Sunderland: Ships fumigated	Sunderland: Rats per ship	Swansea: Ships fumigated	Swansea: Rats per ship	Totals, and av. no. rats per ship, for all ports: Total ships fumigated	Total rats found dead	Av. no. rats per ship
1929	1	50	28	8·0	181	37·0	221	7·80	19	8·74	13	25·9	97	19·8	23	8·20	14	86·3	20	23	617	12,976	21·03
1930	3	22	49	12·2	236	18·0	187	3·50	15	20·0	23	8·9	83	7·0	17	7·6	21	12·2	26	11	660	7,324	11·10
1931	13	10	27	16·6	195	18·1	162	2·02	19	8·0	13	26·8	59	15·0	12	7·5	52	20·0	30	26	582	7,730	13·28
1932	6	51	23	26·2	121	30·8	142	2·03	23	11·2	10	10·1	28	12·1	15	1·6	47	28·9	28	10	443	7,415	16·74
1933	10	12	26	33·2	124	28·5	137	2·05	18	16·2	22	13·9	43	16·8	11	1·09	40	18·7	40	17	471	7,557	16·04
1934	10	12	29	25·5	126	20·5	154	2·06	19	21·0	26	15·3	43	15·5	11	0·09	33	15·7	36	7	487	5,995	12·31
1935	17	18	19	32·8	109	17·5	172	2·09	13	14·0	24	27·5	49	15·2	15	0·86	9	52·3	34	14	461	5,744	12·46
1936	7	6	19	16·1	126	12·0	153	1·75	15	41·5	21	15·8	41	17·6	19	0·68	12	18·5	26	20	439	4,559	10·38
1937	5	7	16	18·3	121	11·0	153	2·29	12	58·4	28	21·5	57	40·6	15	1·3	15	25·0	25	10	447	6,271	14·03

Table 2. *Average number of rats destroyed per ship subjected to measures of rat destruction in all the approved seaports of England and Wales for each year from* 1926 *to* 1936 *inclusive*

(Calculated from the statistics in the Annual Reports of the Chief Medical Officer of the Ministry of Health)

Year	No. of ports concerned	No. of vessels subjected to measures of rat destruction	No. of rats destroyed on ships	Average no. of rats destroyed per ship subjected to rat-destruction
1926	13	3072	52,944	17·23
1927	12	3567	42,473	11·91
1928	12	3420	43,987	12·86
1929	17	4737	52,508	11·08
1930	21	5433	33,978	6·25
1931	21	4429	33,070	7·47
1932	22	5194	32,859	6·33
1933	22	3549	30,503	8·59
1934	23	3351	27,815	8·30
1935	23	3034	23,419	7·72
1936	23	3110	24,876	8·00

tables.) Additional confirmation is supplied by Fig. 2 and Table 2, which show the average number of rats destroyed per ship subjected to measures of rat destruction (trapping, poisoning etc., as well as fumigation) in all the approved seaports of England and Wales, for each year from 1926 to 1936; there has been no decrease in the average number of rats per ship in the period since 1929.

Somewhat different is Fig. 3, which is based on the aggregate statistics

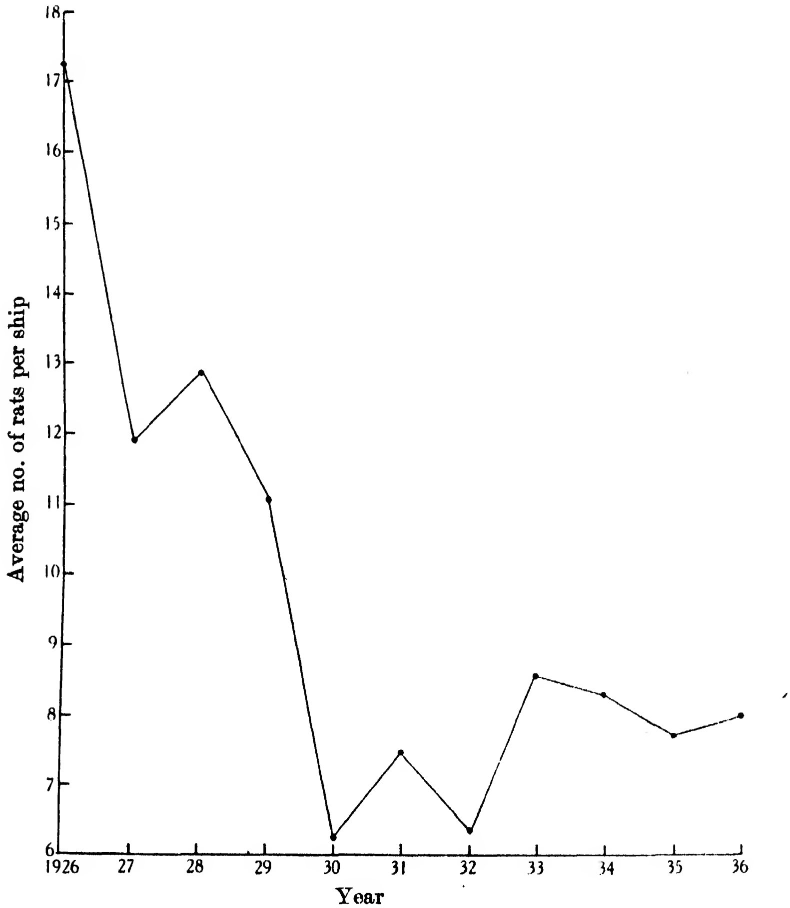


Fig. 2. Average number of rats destroyed per ship subjected to measures of rat-destruction in all the approved seaports of England and Wales, for each year from 1926 to 1936 inclusive.

(Table 3) for the same ports as Fig. 1 (with one omission, for which particulars were not available). This figure shows the number of ships fumigated each year, from 1929 onwards, as a percentage of the total number examined each year for rats. The curve is practically free from fluctuations and shows that, of the vessels examined, the proportion found to require measures of rat destruction is steadily, though now very slowly, decreasing year by year. This conclusion, as Table 3 will show, applies also to most of the ports individually.

Studied in conjunction, then, Figs. 1, 2 and 3, and the corresponding tables,

Table 3. *Number of ships examined for rats, and number of ships fumigated, at nine seaports in England and Wales, in each year from* 1929 *to* 1937

Year	Bristol No. ships examined	Bristol No. ships fumigated	Cardiff No. ships examined	Cardiff No. ships fumigated	Liverpool No. ships examined	Liverpool No. ships fumigated	Manchester No. ships examined	Manchester No. ships fumigated	Middlesbrough No. ships examined	Middlesbrough No. ships fumigated	Newport No. ships examined	Newport No. ships fumigated	Southampton No. ships examined	Southampton No. ships fumigated	Sunderland No. ships examined	Sunderland No. ships fumigated	Swansea No. ships examined	Swansea No. ships fumigated	Total ships examined	Total ships fumigated	% fumigated
1929	2478	28	291	181	335	221	1232	19	93	13	130	97	163	23	482	14	683	20	5887	616	10·46
1930	3378	49	656	236	503	187	1332	15	182	23	145	83	201	17	845	21	578	26	7820	657	8·40
1931	2936	27	602	195	476	162	1359	19	156	13	141	59	212	12	908	52	730	30	7520	569	7·57
1932	2424	23	532	121	489	142	1396	23	161	10	127	28	222	15	880	47	716	28	6947	437	6·29
1933	2127	26	477	124	553	137	1404	18	133	22	126	43	237	11	804	40	793	40	6654	461	6·93
1934	2346	29	454	126	573	154	1514	19	146	26	125	43	283	11	737	33	754	36	6932	477	6·88
1935	2197	19	466	109	562	172	1566	13	169	24	132	49	266	15	814	9	873	34	7045	444	6·30
1936	2284	19	421	126	574	153	1580	15	213	21	101	41	259	19	818	12	819	26	7069	432	6·11
1937	2313	16	409	121	649	153	1654	12	226	28	143	57	230	15	933	15	836	25	7393	442	5·98

Note. Of the ships examined, the percentage requiring fumigation is very gradually decreasing. Table 2 illustrates the same tendency in a different way—the number of "approved" ports rose from 17 in 1929 to 23 in 1936, yet the total number of vessels requiring rat-destruction measures fell from 4737 in the former to 3110 in the latter year.

suggest that the average number of rats per rat-infested ship has of late years been reduced to about the smallest figure practicable at each port under existing conditions; and that an increasing number of ships is found to be free of rat infestation. The latter suggestion is also borne out by the increasing proportion of exemption (as compared with deratization) certificates issued at many British ports to masters of vessels arriving from abroad.

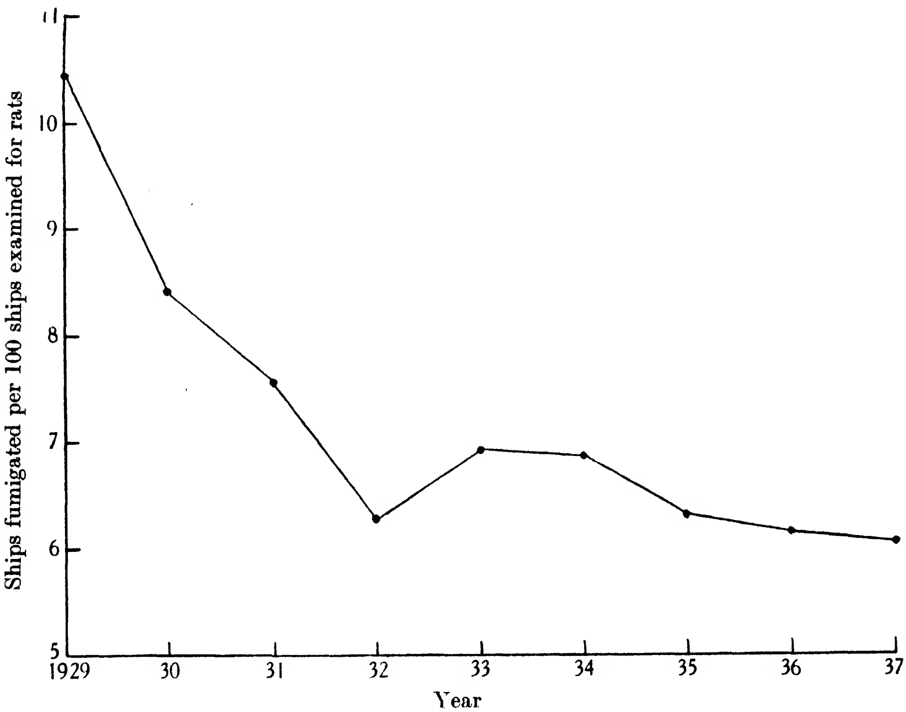


Fig. 3. Number of ships fumigated as a percentage of ships examined for rats, in each year from 1929 to 1937. (Based on the figures for 9 seaports in England and Wales—see Table 3.)

(*b*) *Black rats on shore*

Turning now to the black rats caught on shore in the various Port Health Areas each year, on docks, quays, and in warehouses, etc., it will be seen from Fig. 4 and Table 4 that in the aggregate the numbers show a definite upward tendency. (The part of the curve from and including 1929 onwards is based on the returns for thirteen English and Welsh ports; prior to 1929 the number of ports making returns of black rats caught was smaller.)

Regarding the individual ports, it would appear that with few exceptions, according to the replies received to the questionnaire, no extraneous factors (such as any great variation in the amount of rat-catching), which might significantly affect the figures between 1925 and 1937, are known (see last column, Table 4); so that a definite increase or decrease in the figures should indicate an actual upward or downward tendency of the black rat population in the port concerned. We find, then, that in three of the ports—Grimsby,

Table 4. *Total number of black rats recorded from docks, quays, wharves and in warehouses and other premises ashore at various seaports in England and Wales, in each year from* 1925 *to* 1937

Port	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937	Any known factors affecting figures, e.g. whether rat-catching fluctuated or remained constant
R. Blyth	0	0	0	31	16	34	0	3	0	7	0	0	0	—
Bristol	—	—	—	—	1001	1152	1522	1368	1099	1655	849	592	592	"Fairly constant since 1928"
Cardiff	349	207	343	385	225	454	165	102	—	65	114	92	49	Has remained constant
Dover	0	0	0	0	0	2	0	0	0	0	0	0	0	No information
Grimsby	—	—	940	720	654	786	1170	757	401	1292	988	1137	1224	"Fairly constant"
Liverpool	1699	2165	1651	1947	1324	1637	1405	1968	1849	2479	3074	2870	2454	"Fairly constant over the period mentioned"
Middlesbrough	—	—	0	100	—	6	4	9	54	350	311	216	456	"No known factor"
Newport	24	3	7	1	0	0	0	0	0	0	0	0	0	"Has fluctuated"
Plymouth	—	—	34	97	125	200	205	270	165	96	114	35	21	"Has fluctuated very little"
Southampton	384	397	242	147	290	603	54	11	5	0	0	28	2	"Has remained constant until 1936"
Sunderland	—	26	12	97	92	62	0	24	58	19	16	8	12	"Trapping and poisoning constantly"
Swansea	599	140	236	43	31	74	124	110	175	407	543	543	523	"Fluctuated previous to 1934"
Weymouth	32	41	66	73	352	83	199	189	140	67	20	41	29	"Has remained fairly constant"
Totals	3087	2979	3531	3641	4110	5093	4848	4811	3946	6437	6029	5562	5362	

Liverpool and Middlesbrough—the numbers of black rats taken yearly on shore have increased during the period under review, while in one (Swansea)—having regard to fluctuations in rat-catching previous to 1934, and comparing 1925 and 1937—the numbers seem at any rate not to have decreased.

On the other hand (omitting Dover and one or two others where the data seem rather few to be significant), there are six or seven ports where the figures

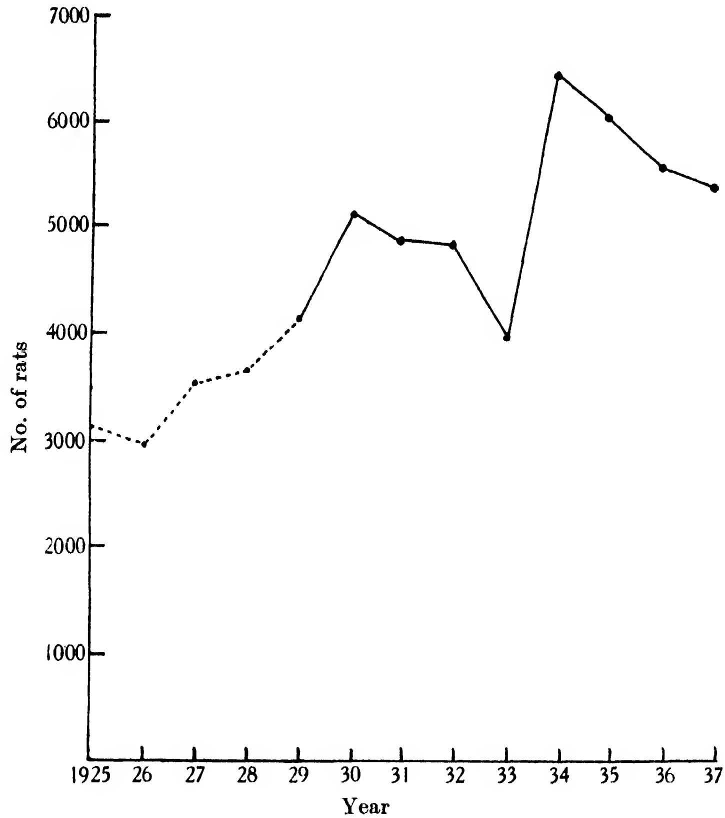


Fig. 4. Total number of black rats recorded from shore premises at the docks each year in a number of British sea-ports. (Since and including 1929 the number of ports is 13; previously it was smaller—see Table 4.)

show more or less clearly a downward trend. This is obvious for example at Cardiff and Southampton over the whole period 1925–37. There are, however, certain facts which must be borne in mind in the case of ports where black rats have decreased at the docks.

(1) In at least one of these ports (Cardiff) there appears to be an established if not increasing population of black rats in the City Area. In each year since and including 1928, the writer has examined a large number of rats from the City of Cardiff (as distinct from those examined from the Port Health Area). In the earlier years of the investigation, the great majority of all rats, whether brown or black, taken by the city rat-catcher were examined in order to collect

their fleas; but latterly, the examination of brown rats has ceased, because sufficient data on their fleas had been obtained, so that since 1934 the only rats examined from the City Area have been black ones. Comparison of the figures for the Port Health Area and for the City indicates that while the black rat has decreased in the former, it has somewhat increased in numbers and range in the latter. The details are as follows:

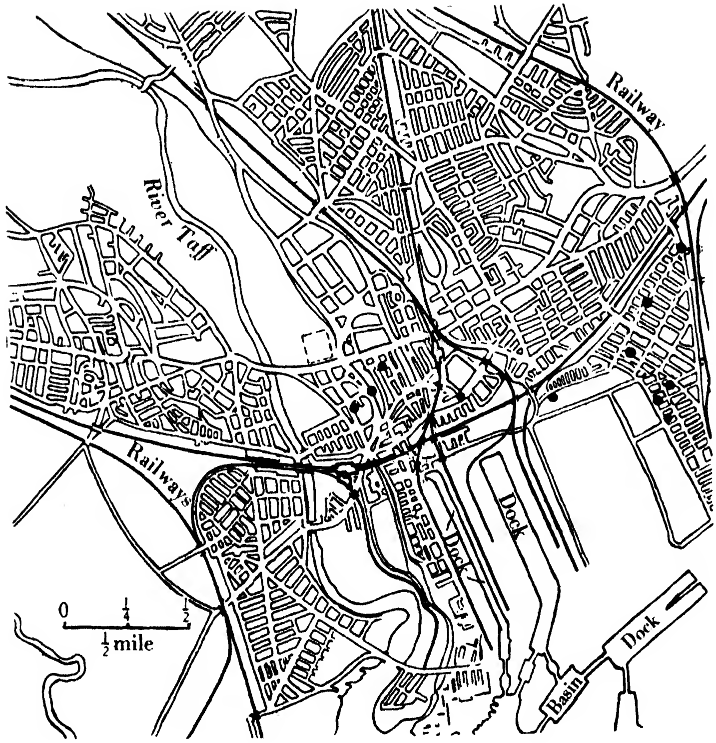
Year	Average no. of rats (*R. rattus*) found dead per ship after fumigation	No. of *R. rattus* identified from docks, quays, wharves, etc., in Port Health Area*	No. of *R. rattus* examined from the City Area
1928	41·8	385	37
1929	37·0	225	38
1930	18·0	454	48
1931	18·1	165	157
1932	30·8	102	71
1933	28·5	—	201
1934	20·5	65	37 (5 months only)
1935	17·5	114	86 (figures incomplete)
1936	12·0	92	121
1937	11·0	49	129
1938	11·0	64	274

* These figures represent only the specimens definitely identified as *R. rattus*. Considerable numbers of rats found dead as the result of baiting are not recorded as to species, but the downward trend of the total figures from year to year is found on comparison to be quite adequately represented by the above series.

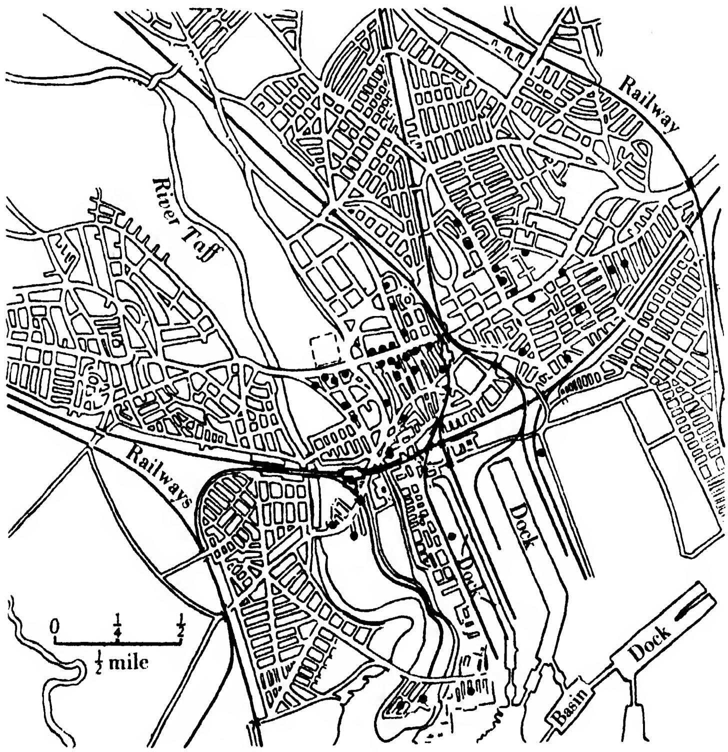
The increase in the numbers of *R. rattus* caught in the city cannot be put down to any intensive development of rat-catching, which has been prosecuted with equal vigour throughout.

Fig. 5 shows that the range of *R. rattus* within the City Area also appears to have increased to some extent. The species has been obtained from various types of premises—private houses, shops, hotels and cafés, cinemas (including one of the most modern in the city, built in 1921), works, a tramway depot, etc.; and in all stages of development. While there is a good deal of evidence for the usual idea that the black rat frequents the upper stories of premises while the brown prefers such places as cellars, this distribution depends, of course, on local conditions. In this connexion reference may be made to Benick's list of the numbers found in each of several types of habitat at Lübeck (**1**). The Cardiff city rat-catcher informs me of one case where brown rats were found in the hollow space under the stage in a cinema, while black ones were living below in the basement—in order, he thinks, to be near the heating apparatus.

Whether the efforts to exterminate the black rat on ships and shore-premises adjoining the docks have driven the species farther afield is a suggestion worth consideration. At any rate, the facts indicate fairly clearly that the reduction of the black rats around the docks has not been accompanied by any reduction of the black rat population in the City Area. This appears to be true even in greater measure of the City of London; I have no actual statistics, but Mr E. C. Read, Chief Rat Officer to the Ministry of Agriculture and Fisheries,



A. 1929.



B. 1938.

Fig. 5. Plan of the city of Cardiff, showing localities from which black rats were received in 1929 (A) and 1938 (B). (*Note*: In both plans only black rats from the City Area, not from the docks, are recorded.)

states in a letter of 3 March 1938: "To my own personal knowledge the rat population of the City of London is approximately 90% *Rattus rattus* with a great preponderance of *alexandrinus*." This, despite the fact that at the Port of London, the average number of rats per ship found dead after fumigation decreased from 12·71 in 1926 to 4·21 in 1936.

There may be other ports in which the black rat is established at a distance from the docks. Liverpool, for example, has a black rat population in the City Area, though this is relatively small and appears to be decreasing: in 1930, of 16,899 rats caught in the City, 2060 were black; in 1931, of 15,755 rats, 1580 were black; in 1934, of 16,687 rats, 1129 were black; while in 1936. out of a total of 14,331, only 456 were of the black species. On the other hand, Liverpool is one of the ports which, as shown in Table 4, still has an undiminished black rat population at the docks.

It is suggested by Hinton (**4**) that the efforts of the black rat to recolonize our cities have been greatly aided in modern times by "rebuilding and the rat-proofing of basements (which has shut out *R. norvegicus*), and by the extension of the telephone system and the removal of kitchens from basements to roofs". And a striking illustration of the position in a large modern American city is afforded by the fact that, of the total number of rats taken by the trappers in San Francisco during the years 1936 and 1937, almost one quarter were *R. rattus*, "found almost exclusively in the section of the city that was rebuilt after the great fire of 1906" (**2**).

There are then several ports in England and Wales which, despite nine to ten years of very efficient ship-deratization work, still have an undiminished if not increasing population of black rats on shore, either around the docks or in the city.

(2) The question also arises whether, in those ports where black rats have decreased on shore premises in the Port Health Area, there has been a *general* decrease of the rat population, both black and brown. If so, then since the brown rat population is essentially a land one, being for example entirely negligible on board ships at ports like Cardiff, Plymouth and River Blyth, it seems clear that the decrease of brown rats on shore does not have much connexion with the decreasing rat-infestation of shipping; and the inference (known to be correct in some cases) is that the decrease of both species around the docks in such ports is due to causes (e.g. improved reconstruction of warehouses, etc.) other than ship-deratization measures. In these ports, then, where the black rat population on shore at the docks has decreased, the suggestion that this population is mainly derived from ships and has declined as a result of modern ship-deratization, though possibly valid in some cases, receives actual support from the statistics only where the decrease in the black rats is not accompanied by any decrease in the brown; the only cases of this kind, among the ports supplying information, being Bristol and Sunderland.

4. Scotland and Ireland

Black rats on ships and ashore

The Scottish ports from which replies were received to the questionnaire were Edinburgh, Glasgow, Dundee, Ayr, Grangemouth and Greenock. Glasgow is, however, the only one to supply data that are readily comparable throughout with those for the English and Welsh ports, particularly on the main point at issue—the status of *R. rattus* ashore. The data may be tabulated as follows:

Year	No. of ships examined for rats	No. of ships fumigated	Average no. of dead rats per ship after fumigation	No. of black rats destroyed on docks, quays, wharves and in warehouses, etc.
1929	1651	127	17	97
1930	1625	127	17	371
1931	1451	173	12	97
1932	1394	119	13	46
1933	1404	112	18	150
1934	1513	126	17	306
1935	1510	107	26	503
1936	1564	130	27	732
1937	1624	133	19	618

Regarding the figures for ship fumigation, Dr A. S. Macgregor, the Medical Officer of Health, observes: "In the table given above there is an increase in the number of rats per ship during the past three years and this, it is stated, may be due to more foreign ships being dealt with, especially those of Greek registration."

With reference to the position on shore, "the assistant inspector who immediately supervises the fumigation of ships states that outside the docks he has seldom or never seen black rats. The number of rats in the docks, he says, varies from time to time with the cargoes that may be brought in from ships which are either ratty or not." It will be noted that the number of black rats taken annually on shore premises, which does not appear to be decreasing, has in fact been particularly large during the last three years, these being also the years when the average number of rats per ship fumigated was highest.

At Dundee, figures are available for the black and brown rats taken on shore premises in the Port Area for the three years 1935–7; previously only the total number of rats, irrespective of species, having been recorded. In 1935, 406 brown rats were taken and only 4 black; in 1936, 164 brown and 10 black; in 1937, there were only 126 brown rats but the black had increased to 62.

The only replies received from Ireland to the questionnaire were from Dublin and Belfast. At Dublin the number of ships fumigated, and the average number of rats found dead per ship, are very small—about two ships per year, with an average of only two to three rats per ship; as the Medical Officer observes, the greater proportion of foreign ships make their first call at English ports, where rigid preventive measures are in operation, while in other ports

trading with Dublin large staffs are employed for the purpose. "There is, therefore," he says, "a very appreciable lessening of our deratization measures on these vessels." Nevertheless, on shore, from 1932 to 1937 inclusive, 71,580 rats were destroyed on docks, quays, wharves, etc., at Dublin; this large number being mainly accounted for by the fact that during the years 1933 to 1936 "the Dublin Port and Docks Board (the governing body of the entire dock system) engaged the services of a contractor to carry out rat-repression methods"; it is stated that of the total "about 80% belonged to the brown variety". *R. rattus* must still be common enough on shore if about 14,000 of them were accounted for during those six years.

With regard to Belfast, the data relevant to the present enquiry may be tabulated thus:

Year	No. of ships examined for rats	No. of ships fumigated	Average no. of dead rats per ship after fumigation	No. of black rats destroyed on docks, quays, wharves and in warehouses, etc.
1929	59	13	14	72
1930	97	23	3	91
1931	66	20	12	210
1932	68	12	7	302
1933	77	7	5	222
1934	63	9	5	213
1935	54	3	9	261
1936	75	7	6	164
1937	74	5	2	286

Here, again, the number of black rats destroyed on shore shows no sign of a decrease during the past nine years, although the amount of rat-catching conducted is stated to have been "fairly constant" over that period.

5. RELATIVE NUMBERS OF THE THREE SUBSPECIES OF *RATTUS RATTUS*

As is well known, the species *R. rattus* occurs on ships and on shore in Europe in three definite colour and pelage phases, which may be regarded as subspecies; *R. r. rattus*, with black back and smoky grey belly, a type characteristic of, and probably originating in, the cold temperate countries of Europe; *R. r. alexandrinus*, with brownish grey back and dingy belly, a type particularly characteristic of Asia Minor and North Africa; and *R. r. frugivorus*—in which the brighter brown of the back is separated by a sharp line from the pure white of the belly—distributed widely in the Mediterranean region.

Statistics are available from four of the ports as to the relative numbers of each subspecies found there, and although the differentiation is usually done by the lay staff, a fact which should be borne in mind when considering the figures, it is quite easy with a little practice to distinguish the three types. The writer has for years been able to assign this task to a lay member of the staff of his own department, knowing from experience that mistakes were of very rare occurrence.

Mr E. C. Read's statement that the great majority of the black rats taken in the City of London are of the subspecies *alexandrinus* has already been mentioned, and so far back as 1890, it would seem from a note in *The Zoologist* of that year (p. 135), a considerable number of the rats at Jamrach's animal establishment in East London were of the *alexandrinus* type. Of six specimens kindly sent to me by Messrs Wm. Dalton and Sons as a sample of the City of London rat population, only one was a typical *rattus*, three were typical *alexandrinus*, while two appeared to be crosses. At Plymouth *alexandrinus* is also said to be the most numerous to-day: the Deputy Medical Officer states, in reply to the questionnaire, that *R. r. alexandrinus* is the type "most commonly met with; *R. r. rattus* to some extent; *R. r. frugivorus* not noticed".

At Glasgow, Liverpool, Hull, and Cardiff the state of affairs, as shown by records extending over a period of nine years or longer, is somewhat different. At Glasgow the total numbers of each subspecies (from ships and docks), destroyed during the years 1929–37 inclusive, were as follows; *R. r. rattus*, 10,526; *R. r. alexandrinus*, 9960; *R. r. frugivorus*, 9627; each being the most numerous in three out of the nine years. The three forms therefore appear to occur with about equal frequency, the typically northern form *rattus*, the so-called "old English black rat", which was our common British rat until about two hundred years ago, being slightly the most numerous.

At Liverpool the figures for *R. r. rattus* only are given separately, those for the other two subspecies being combined. From 1930 to 1937 inclusive *rattus* numbered 18,966, while *alexandrinus* and *frugivorus* together numbered 20,962; it would appear therefore that *rattus* is definitely predominant at Liverpool. Similarly, the figures for Hull and Goole, which go back to 1925, show a total of 40,110 *rattus* and only 22,649 of the other subspecies; *rattus* being the most common in 10 out of the 13 years.

At Cardiff, the writer has kept records of the numbers of each subspecies he has examined from the Port from 1926 to 1938, and has also some data for previous years. The total numbers of each, from ships and docks, warehouses, etc. in the Port Health Area, examined in the Department of Zoology at the National Museum of Wales during this period were—*R. r. rattus*, 1711, *alexandrinus*, 434; *frugivorus*, 1029. From the City, as apart from the Port Area, the numbers examined were: *rattus*, 876; *alexandrinus*, 84; *frugivorus*, 351. It is clear that, both at the docks and within the city, *rattus* is the most numerous, *frugivorus* fairly common, while *alexandrinus*, contrary to the state of affairs described at London and Plymouth, is quite definitely the rarest instead of the commonest type. This holds not only for the aggregate figures but from year to year; in 14 out of the 17 years 1922–38, *rattus* was the most, and *alexandrinus* the least numerous among the specimens received from the Port; while during the eleven years in which rats have been examined from the City Area, *rattus* was the commonest throughout and *alexandrinus* the scarcest.

In brief, therefore, at three ports on the west coast—Glasgow, Liverpool

and Cardiff—and at Hull on the north-east coast, *rattus* is in greater or less degree the dominant subspecies, whereas in London and Plymouth *alexandrinus* is stated to occupy this position. Whether it would be possible to establish any connexion between the form of black rat chiefly found at a port, and the type and nationality of the bulk of the shipping there, is an interesting speculation, but one which is outside the scope of the present paper.

The subspecies of the black rat formerly found in London, as in other parts of Great Britain, was the "old English black rat", *R. r. rattus*; the fact that *alexandrinus* is now the most frequent there suggests that the black rat population of modern London originated in the first place from shipping, and not from any revival within the city of the old type; but however it originated, it seems now to be firmly established without requiring any augmentation from the rapidly dwindling numbers of ship rats.

6. SUMMARY

Statistics are given to show that the average number of rats (which are almost invariably black rats) per ship fumigated at British ports, and the percentage of shipping requiring fumigation, have declined considerably within the 13 years 1925–37; while many precautions are taken to prevent, as far as possible, the passage of rats between ship and shore.

Despite this, several ports still show an undiminished black rat population on shore—at the docks and, in some cases, in premises at a distance from the docks. In those ports which show a decrease in the black rat population on shore, comparison with the figures for brown rats indicates in most cases that the decrease applies to both species, and is not therefore necessarily related to ship deratization measures.

It seems clear therefore that the black rat is capable of maintaining itself in some numbers in various types of premises at British seaports, without receiving any notable additions to its numbers from ships.

From statistics quoted, it appears that *R. r. rattus* is in greater or less measure the most frequent subspecies found at three ports on the west and one on the north-east coast; whereas at London and Plymouth the commonest subspecies is stated to be *alexandrinus*.

REFERENCES

1. **Benick, L. (1924).** "Über das vorkommen der Haus- und Dachratte in Lübeck." Mitt. geogr. Ges. Lübeck, 2nd ser., 29: 85–90.
2. **Eskey, C. R. (1938).** "Flea infestation of domestic rats in San Francisco, Calif." U.S. Publ. Hlth Rep. 53: 948–51.
3. **Henderson, J. & Craig, E. L. (1932).** "Economic mammalogy," p. 292. London.
4. **Hinton, M. A. C. (1931).** "Rats and mice as enemies of mankind." Brit. Mus. (Nat. Hist.), Econ. Ser. no. 8, 3rd ed., p. 5.
5. **Jackson, J. W. (1929).** "Report on the animal remains found in the Kilgreany cave, Co. Waterford." Proc. Speleol. Soc., Bristol, 3: 137–52.
6. **Matheson, C. (1931).** "The brown and the black rat in Wales." National Museum of Wales.
7. **Patterson, A. H.** Notes and papers in Zoologist, 1898: 299–310; 1906: 71; 1912: 417–23.
8. **Southwell, T. (1896).** "*Mus rattus* at Great Yarmouth." Zoologist: 143.

AN ATTEMPT TO DETERMINE THE ABSOLUTE NUMBER OF RATS ON A GIVEN AREA

By P. H. LESLIE and D. H. S. DAVIS

From the Bureau of Animal Population, Oxford University, and the Sir Alfred Lewis Jones Research Laboratory, Freetown, Sierra Leone

(*With 3 Figures in the Text*)

CONTENTS

		PAGE
1.	Introduction	94
2.	Field observations	95
3.	General conceptions	98
4.	Theoretical	101
5.	Arithmetical analysis	106
6.	Discussion	110
7.	Summary	113
8.	Acknowledgements	113
	References	113

1. Introduction

One of the most interesting problems for the ecologist is the estimation of the density of a particular animal species and in an attempt to determine this a system of trapping is among the devices most commonly employed. The reaction between a number of traps and a population of animals is essentially a special case of the predator-prey relationship; and perhaps it would not be too much to say that the experimental study of this trap-animal reaction is fundamental to the development of quantitative ecology in the field. The proper procedure would be to formulate a theory of trapping in the simplest terms possible and then to experiment with a given number of animals under known conditions. On the comparison of the results with the equations deduced from theory would depend whether the hypothesis be accepted or recast. The observations discussed in this paper were made in order to see whether any consistent results could be obtained by means of a standardized trapping method: they are not experiments in the sense we have outlined since the number of animals at risk was unknown. But, although a number of details will be noticed in which, from this point of view, an improvement or economy of design might have been achieved, the design as a whole fulfilled certain essential conditions of such an experiment. It is interesting to observe that the arithmetical analysis of this data has not revealed any result which

is inconsistent with the fundamental hypothesis. Logically this does not mean that its truth is to be accepted; indeed it would be surprising if such an elementary theory should prove a sufficient explanation of what must necessarily be a most complex relationship. The most that can be said of these results is that they appear promising, and it is in the hope of stimulating further work on the lines we have indicated that they are discussed in some detail.

2. Field observations

The field observations were carried out in Freetown, Sierra Leone, during the dry season in February and March 1937. An area of 22·5 acres, defined by the ordinates of the survey map, was chosen as being a typical block of houses occupied by natives. It contained, as will be seen from the map (Fig. 1), no open spaces such as, for example, parks, railway sidings or foreshore, and was inhabited for the most part by a more intelligent type of native than other possible quarters of the town. This is an important point, since the success of an extensive trapping experiment will depend on the intelligent co-operation between assistants and inhabitants. Although the possibility of interference with the traps by the natives cannot be wholly eliminated, we consider that in the present instance this disturbing factor was reduced to a minimum.

The experiment was carried out in the following way. A plan was made and the area then divided into two roughly by the line Lewis Street—George Street West. Scattered over the half-area below the division line 35 houses were chosen from the plan, and on the first evening three traps were set in each house, left for the twelve hours of darkness and collected in the morning. The next night 35 houses in the other half were similarly treated. On the third night a return was made to the bottom half of the plan; on the fourth to the top half and so on alternately up to the sixth night. 35 new houses were trapped on each occasion and these were chosen so far as was possible adjacent to those trapped on the night when the half-area was previously visited. The buildings varied in size, ranging up to three stories, and the three traps were distributed among the various floors. There was then a pause for one night and on the eighth day the rotation of sites was restarted, wherever possible using the same houses as were trapped during the first week. If for any reason a particular house could not be revisited, an alternative one was substituted in its stead. The whole experiment lasted for a period of six weeks, and during each week 630 traps were set in 210 houses.

The traps were of the "breakback" variety, which is generally considered to be the most efficient, and only one animal could be taken in each. They were made by the French firm, "Manufactures des armes et des cycles", Loire, and consisted of two semicircles of stout wire joined across the diameter by a spring. When set a circle is formed with the bait on a trigger in the centre and the two semicircles spring together when the trigger is released. Slices of

cassava (*Manihot utilissima*) were employed as bait. The actual process of setting and collection had to be entrusted to native assistants and from D. H. S. D's. experience of them we are reasonably certain that the work was efficiently carried out. They also entered in a book the results from each house and there

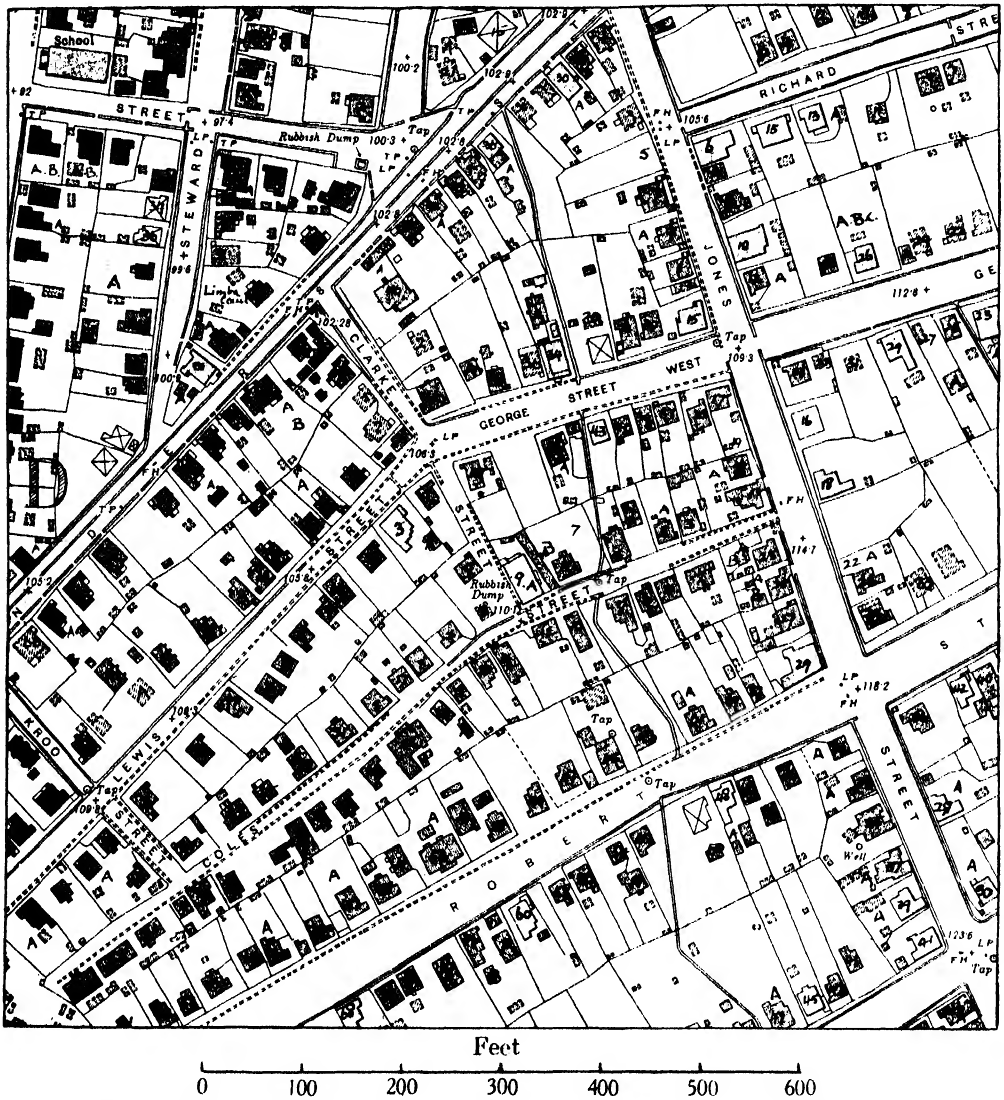


Fig. 1. Map of the area trapped. (Reproduced by permission of the Director of Surveys, Freetown.)

are a few indications of possible errors in bookkeeping, e.g. rats entered as being trapped at the wrong address. This is however a small matter, as we are not concerned with the results from the individual houses, but rather with the total catch. This was checked in the laboratory where the rats were typed, sexed and so on by D. H. S. D. There remains the question of those traps, either with or without bait, which were found sprung and containing no rat or other

animal. Undoubtedly the greater proportion of these were sprung either accidentally by members of the household, stray dogs, cats, hens, etc., or by the rats themselves who managed to avoid capture: but also a number may actually have trapped rats, which were afterwards either thrown away by the inhabitants or eaten, for example, by cats. Both of these latter alternatives were reported to have occurred on three occasions during this series, and it is always possible that further instances may have been overlooked by the assistants or concealed from them by the inhabitants concerned. But such sources of error are inherent in the conditions under which this experiment was done, and provided this accidental or purposeful sabotage—if one might so term it—remains on a relatively small scale, allowance can always be made for it in the final calculations. It is most unfortunate that we have no records for this series of the number of such negative-sprung traps and, as will be seen later, we have been compelled to adopt an average figure derived from a similar type of experiment on another area in Freetown. Possibly we have painted the picture blacker than it actually was: in our judgement the figures reported in this paper were the results of efficient trapping and such errors as may have occurred were relatively unimportant.

The sum of the first two nights' results from 210 traps set in 70 houses represents the first trapping of the whole area: the sum of the third and fourth nights' the second trapping: and so on. The results are given in Table 1. The most frequent type to be captured was *Rattus rattus*; but in addition a number

Table 1

Trapping no.	Number trapped: *R. rattus*	Other species: *RN*	*MM*	*C*	*M*	Total	Weekly total of: *R. rattus*	Other species	Total no. *R. rattus* trapped
1	49	7	3	.	.	10			
2	32	4	3	.	.	7			
3	31	5	7	.	.	12	112	29	112
4	34	5	4	.	.	9			
5	16	8	1	.	.	9			
6	33	7	2	.	.	9	83	27	195
7	22	5	1	.	.	6			
8	27	4	5	.	.	9			
9	17	5	11	.	.	16	66	31	261
10	19	1	3	1	.	5			
11	18	10	3	.	1	14			
12	16	3	3	1	.	7	53	26	314
13	18	2	2	.	.	4			
14	12	1	2	.	.	3			
15	14	1	5	.	.	6	44	13	358
16	12	3	2	1	.	6			
17	17	3	2	.	.	5			
18	7	2	5	.	.	7	36	18	394

210 traps were set on each occasion.

RN = *Rattus norvegicus* *C* = *Crocidura*
MM = *Mus musculus* *M* = *Mastomys*

of traps were occupied by other species, by far the greater part being *R. norvegicus* and *Mus musculus*. From the weekly totals it is seen that these are relatively much less numerous than *Rattus rattus* and this latter type may be regarded as the principal rodent infesting this block of property. In order to avoid any misconceptions it might be as well to point out that they are not confined to the houses. A fortnight after this series was ended the area was treated with the same rotation of sites, only the traps were set in the compounds instead of in the houses. The number of traps set was 630 and 32 *rattus* were captured; a figure which agrees very well with the last weekly total for the

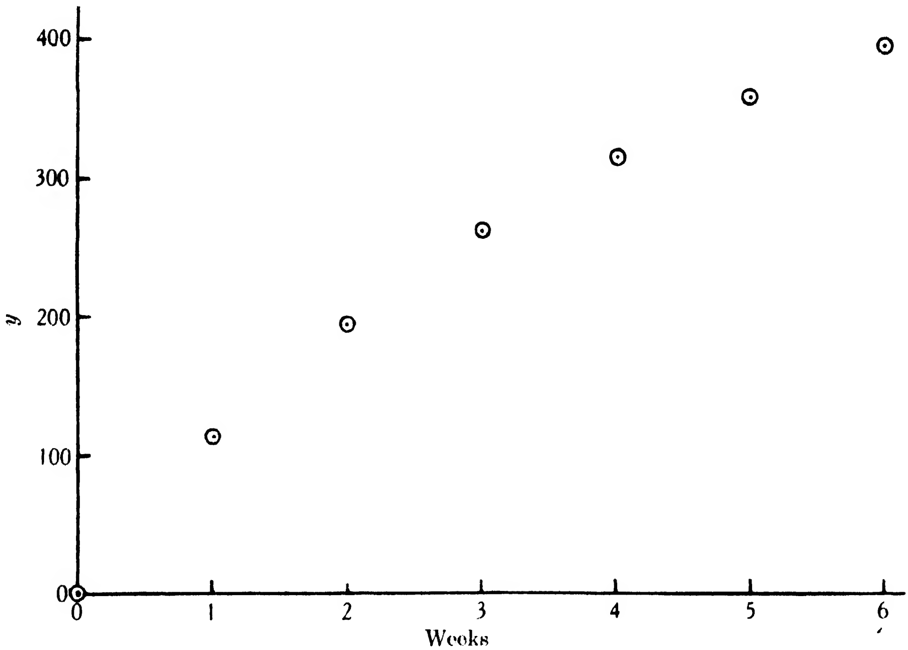


Fig. 2. The total number of *R. rattus* (y) which were trapped plotted as a function of time.

house-trapping, namely 36. The last column of Table 1 gives the total number of *rattus* trapped up to the end of each week, and when these figures are plotted as a function of time, it will be seen from Fig. 2 that they form an extraordinarily smooth curve. It was this suggestion of an underlying law and order that prompted a more detailed analysis.

3. General conceptions

Reduced to essentials, a number of animals is imagined to start their search for food at different points over an area. Supposing that in the type of animal society we are considering each individual searches independently from the others, the movements of the population may be said to be unorganized or in other words at random. During their search a certain number of traps

are encountered. This conception of a number of individuals moving over a topographic field and suffering a number of random collisions with other animals or objects in their environment, has the merits of simplicity and has been employed by many authors, e.g. Lotka (1925) and Volterra (1931), in the mathematical treatment of population questions. As Lotka (1925, p. 358) has pointed out: "we might seek to develop, for such a system, a discipline of statistical mechanics similar to that which the physicist has developed to deal with the kinetic theory of gases and allied problems."

In the type of system dealt with here, there are in reality two separate areas to consider: the area bounded by the extreme limits of the individual paths of search, within which the population may be said to be moving at random, and the area within which all the traps lie. In the case of an island, for instance, it is easy to see that the two areas can be made to coincide and the total population will then be exposed to risk. But where there are no topographical features to form a barrier to the movements of the individuals and when the same trap-boundaries are used repeatedly, the relation between the two areas becomes of some importance. The area of search for food over a period of time will depend on the habit of the species; whether it be migrant or having some fixed point such as a nest or lair to which it returns. In the case of the rat when the population is in a settled condition—neglecting, that is to say, the migratory movements which are reported to occur from time to time—the individuals leave their holes and return again to the same point or at any rate a point very close to where they started. By making the dimensions of the trap area large relative to the average radius of movement of a rat, it is thus possible to include within its bounds, as in an imaginary island, an unknown number of individuals. The overlap, which must always occur with surrounding areas, can now be considered negligible. The experience of Petrie & Todd (1923) in Egypt, where *R. rattus* were trapped alive, marked and then released, was that the movements of recaptured animals over a period of three months were limited, consisting for the most part of oscillations between two or three adjacent houses. They noted also that intensive trapping did not apparently disturb the population and that the broader streets appeared to act as a natural barrier to their movements. Although we can produce no definite measurements in support of the statement, there is no reason to suppose that the movements of *R. rattus* in Freetown were any different from those of their brethren in Egypt. This point will be returned to later in the section devoted to the arithmetical analysis of the results: for the moment it will be assumed that the furthest distance reached by any one rat during its search for food was small compared to the dimensions of the trapping area.

There is in addition another important point to be considered; whether the population at risk was distributed at random over the area. During a week 210 houses were trapped and up to three rats could be captured in each. If $H=$ the number of houses and $R=$ the number of *rattus* trapped during any

one week, the mean number of rats per house $= R/H = m$. Then under the hypothesis of a random distribution, the number of houses which should have 0, 1, 2 and 3 rats can be calculated by means of the successive terms

$$He^{-m}\left(1,\ m,\ \frac{m^2}{2!},\ \frac{m^3}{3!}\right).$$

In Table 2 are given the number expected from this Poisson series, together with the numbers observed. The first two weeks' results are tabulated separately; while the remaining weeks have been added together in order to obtain

Table 2

No. *rattus* per house	Week 1, 112 *rattus*: Obs. no. houses	Exp. no. houses	Week 2, 83 *rattus*: Obs. no. houses	Exp. no. houses	Weeks 3, 4, 5 and 6, 199 *rattus*: Obs. no. houses	Exp. no. houses
0	129	122·3	136	140·5	656	661·8
1	54	65·5	65	55·8	169	157·0
2	20	17·6	6	11·1	12	18·6
3	6	3·1	2	1·5	2	1·5
Total	209	208·5	209	208·9	839	838·9
	$\chi^2 = 3{\cdot}743$, $n = 1$, $P = <0{\cdot}10, >0{\cdot}05$		$\chi^2 = 3{\cdot}340$, $n = 1$, $P = <0{\cdot}10, >0{\cdot}05$		$\chi^2 = 2{\cdot}819$, $n = 1$, $P = <0{\cdot}10, >0{\cdot}05$	

Total $\chi^2 = 9{\cdot}902$; $n = 3$; $P = <0{\cdot}02, >0{\cdot}01$

In calculating χ^2 the 2- and 3-*rattus* houses were added together.

figures of a convenient magnitude in the 2-3-rat classes. Three houses were reported as having "rats" thrown away by the householders or eaten by cats, and since it is impossible to know whether these referred to *rattus* or *norvegicus*, they were left out of the calculations. The agreement between the expected and observed numbers is fairly close and the values of χ^2 fall just below the conventional level of $P = 0{\cdot}05$ in each of the three distributions. However when the three values are added together giving $\chi^2 = 9{\cdot}902$ and $n = 3$, $P =$ just $< 0{\cdot}02$; so that there is a suggestion of some slight disturbing influence on the random distribution. Possibly this may be due to errors of book-keeping or to the negative-sprung traps which have been previously mentioned; since for the purposes of this test we have assumed the complete efficiency of all the traps. Whatever the reason, the degree of departure from randomness is not sufficient to cause us to abandon any further application of the theory to these figures.

Lastly, there is the question of the relationship between the minimum number of hours during which every individual member of the population will have been exposed to risk and the time during which the area was trapped each night. Obviously in the design of any experiment it is desirable to have a conformity between these two times similar to that between the two areas discussed previously. Very little seems to be known about the activity of

the rat in the wild state. It has been shown by Richter (1927) that white rats in the laboratory have approximately a four-hourly rhythm of activity when food is present in the cages; when it is absent this period becomes shorter and Richter suggests that this restlessness and activity is associated with spasmodic contractions of the empty stomach. Supposing that the same conditions hold good in the field; and taking into consideration that the wild rat must search for food: then it appears a fair assumption to make that during a night every individual—apart from the young in the nests—will pass some period of time on the surface and therefore at the risk of being trapped. We are well aware that this is rather a sweeping assumption, to which a number of objections can easily be raised: but in the present state of our knowledge we submit that, for the purposes of this argument, it is good enough as a first approximation to the truth.

To summarize this section: the conception has been formed of an area being searched in a random fashion by a population which remained circumscribed over the period of the experiment owing to its habit of life. Moreover it is assumed that during any one night every individual rat inhabiting the half-area trapped will have been exposed to the risk of capture.

4. THEORETICAL

The area defined by the map ordinates, to which strictly speaking should be added the floor area of the second and third stories, will be regarded as a unit area and the number of hours of darkness elapsing between setting and lifting the traps as a unit of time.

Let a quantity p be defined as the probable value of the path an animal can traverse without colliding with a trap, i.e. the mean free path. Then, by the well-known theorem, the probability P that a single animal moving among a number of traps at rest will traverse a distance x without a collision, is

$$P = e^{-x/p}. \qquad \ldots\ldots(1)$$

Suppose that on the unit area there are T traps. Let the area be divided into T small squares, each of which on the average contains one trap. Let x be the length of the side of each of these squares; then one trap is contained in an area of x^2 and x is also the average distance between adjacent traps. It follows that $Tx^2 = 1$. Let r be the radius of the field of influence surrounding each baited trap and suppose that any animal which is within this imaginary circle will respond to the stimulus received through its senses by moving towards the centre. Then an animal may be said to have discovered or collided with any trap lying within a distance r from itself. If it moves over a distance x, which for the sake of simplicity is taken to be a straight line, it will search an area $2rx$ and will collide with any trap lying within this parallelogram. Since one trap is contained in the area x^2, the probability that there is a trap

on the area $2rx$ is $2rx/x^2$ and therefore the probability of there being no trap, i.e. no collision, is $1-2rx/x^2$. From (1)

$$e^{-x/p} = 1-\frac{2r}{x},$$

or, expanding $\log_e\left(1-\frac{2r}{x}\right)$ in series,

$$\frac{x}{p}=\frac{2r}{x}+\frac{1}{2}\left(\frac{2r}{x}\right)^2+\frac{1}{3}\left(\frac{2r}{x}\right)^3+\text{etc.}$$

In the conditions of an experiment like the one we are considering, r must be small compared with the average distance between adjacent traps. It follows that $2r/x$ is a small quantity compared with unity and therefore its square, cube, etc. can be neglected. The expression above then reduces to

$$\frac{x}{p}=\frac{2r}{x},$$

and since $Tx^2=1$

$$p=\frac{1}{2rT}. \qquad \text{......(2)}$$

Although its movement may be intermittent, an animal during a unit of time will cover a certain distance which can be termed its velocity v. The probable number of collisions which it will make is

$$\frac{v}{p}=v2rT.$$

Suppose that there are N animals on the area and that all these individuals are exposed to risk during some period of a unit of time. Now it will be very unlikely that the quantities $v_1, v_2, v_3, \ldots, v_N$ will all be the same, but it is convenient to make the simplifying assumption that they are. When in the molecular theory of gases the velocities of the individual molecules are assumed to be distributed according to the Maxwellian law, it is found that the equation defining the probable value of the mean free path differs only by a constant ($\sqrt{2}$) from that arrived at when the velocities are assumed to be the same. We can therefore say either that the N individuals move with the same velocity V; or, better, regard the quantity V as an average value defining some unknown distribution, equivalent to the Maxwellian,[1] which is assumed to be constant and independent of any factor such as the age distribution of the population. The N animals will therefore in a unit of time suffer $V2rTN$ collisions with traps.

[1] Working in two dimensions, the equivalent distribution to the Maxwellian would be that the number of animals having a velocity between v and $v+dv$ is assumed to be given by

$$dN=2Nh^2v\,e^{-h^2v^2}\,dv.$$

As a matter of interest it might be mentioned in passing that we have recently observed this distribution to be realized very closely in a similar type of problem, namely the distances, measured in a straight line, between the points at which long-tailed field-mice (*Apodemus sylvaticus*) were trapped alive and subsequently recaptured.

In general it will not be true that every collision results in the capture of an animal. Even if the traps are mechanically efficient and properly set, it may still happen that owing to the design of the trap an animal, in order to spring it, must approach in a particular way. Let c be the fraction of collisions which result in capture; then c may be called a measure of the efficiency of the traps. In future we shall employ the word "collision" in the sense of "effective collision".

Suppose for the moment that trapping is a continuous process which is not terminated at the end of each unit of time by the removal of the traps. Let y be the total number of animals trapped up to the time t and N be the initial population on the area. In addition assume that the population does not increase through young leaving the nest and immigration, or decrease through normal deaths and emigration during the time of the experiment. Then at the time t there will be $N-y$ animals and $T-y$ traps left. In the interval of time $t+dt$ the $N-y$ animals will make $cV2r\,(T-y)\,(N-y)\,dt$ collisions with the remaining traps and this quantity must equal the dy animals captured. We have, therefore, putting the constant $cV2r=s$,

$$\frac{dy}{dt}=s\,(T-y)\,(N-y), \qquad \ldots\ldots(3)$$

which gives on integration

$$\frac{T-y}{N-y}=\frac{T}{N}e^{-s\,(N-T)\,t}. \qquad \ldots\ldots(4)$$

In the case of a planned experiment, where the initial number of animals is known, this equation should express the interaction between animals and traps, if the assumptions made as to the random nature of collisions and the constant mean velocity of the individuals hold good. But in the absence of any knowledge about the value of N and given only the value of y at the end of one unit of time, as in the present series of results, little use can be made of it and we must proceed somewhat differently.[1]

In the differential equation (3) instead of the variable $(T-y)$ put $T=$ the number of traps set and keep it constant. This is the same thing as assuming that the "breakback" traps, which can catch only one individual, have become

[1] In the first part of this theory which is merely an adaptation in two dimensions of the elementary kinetic theory of gases, we have borrowed freely from various sources, e.g. Lotka (1925) and Mellor's *Higher Mathematics for Students of Physics and Chemistry*, and reference may be made to these or to any textbook of physical chemistry for further details. It should be noted that if rats be regarded as prey and traps as predators, both equations (4) and (5) can be derived immediately from the well-known Lotka-Volterra system of simultaneous equations, $dN_1/dt=(a_1-b_1N_2)\,N_1$, $dN_2/dt=(-a_2+b_2N_1)\,N_2$, where a_1, a_2, b_1, b_2 are constants and N_1 and N_2 are the number of prey and predators respectively: in the case of (4) by putting $a_1=a_2=0$ and $b_2=-b_1$; and in the case of (5) $a_1=0$, $dN_2/dt=0$. But it seemed advisable to give the development of this special case of the predator-prey relationship in full for the sake of clarity, and in order that the biological significance which is attached to the various constants may be of assistance in the design of any future experiment.

a type of cage-trap, catching any number, and that all the collisions which are made by chance with a trap already occupied result in capture. Putting $sT = k$

$$\frac{dy}{dt} = k(N - y),$$

whence
$$y = N(1 - e^{-kt}). \qquad \ldots\ldots(5)$$

It follows from this equation that during one unit of time there would occur $N(1 - e^{-k})$ collisions and this quantity would represent the number trapped if all the collisions were able to take place. Let

$$1 - e^{-k} = k'.$$

The average number of collisions per trap is $k'N/T$ and, since it has been assumed that the collisions take place at random, it follows from the Poisson distribution that the proportion of traps which suffer 0, 1, 2, etc. collisions will be given by

$$e^{-k'N/T}, \quad \frac{k'N}{T} e^{-k'N/T}, \quad \frac{1}{2!}\left(\frac{k'N}{T}\right)^2 e^{-k'N/T}, \text{ etc.}$$

The first collision results in the trapping of an animal and any second or more collisions on that trap are ineffective. Those animals which might have been captured at this point are therefore free to collide with other unoccupied traps. But if $k'N < T$, the proportion of traps which would be expected to suffer two or more collisions is small compared with the proportion which suffer none or only one: therefore the number of animals which collides by chance with an occupied trap is small and the possibility that these animals manage to collide with unoccupied traps during the time left to them, might be considered negligible. An imaginary numerical example will perhaps make this point clear. If $k'N/T = 0{\cdot}281$ and $T = 200$, the expected number of traps which will suffer no collision is 151·0; one collision, 42·4; two collisions, 6·0; and three collisions, 0·6. Had all these resulted in capture we should have expected 56 animals to have been trapped; actually only 49 could have been owing to the type of trap. There were therefore seven animals which during the course of the night collided with traps already occupied and were then free to make contact with the remaining unoccupied ones. If we assume, taking into account their velocity and the average distance between traps, that it is very unlikely that they will have managed to do so during the time left before the night's experiment was ended, then, putting R = the number of *rattus* captured, the proportion of unoccupied traps,

$$\frac{T - R}{T} = e^{-k'N/T}. \qquad \ldots\ldots(6)$$

With regard to the present experiment there are two further complications which have to be taken into account: a certain number of traps were occupied

by other species and others were found sprung and containing no animal in the morning. Both these factors act in the same way by preventing *rattus* being caught by these particular traps. Apart from those which actually caught *rattus*, the initial number of traps (T) is being decreased throughout any one night by the action of these outside agencies. Let b equal the number of traps occupied by other species and found negatively sprung; then provided that b be relatively small compared with T, it will be sufficiently accurate for our purpose to assume that the number of traps set, which we have taken as constant in equation (5), can be described by a decreasing linear function of time, say $T-bt$. It follows that the average number of traps per unit time which are free to catch *rattus* is $T-b/2$. Let $b/2=n$: then had there been only *rattus* present on the area and no negative sprung traps, we should have expected the n traps to have caught the same proportion as the $T-n$, i.e. $nR/T-n$. For instance on the first trapping of the area, $T=210$, $n=26$ and 49 *rattus* were trapped; $49/184=0{\cdot}2663$ and we should have expected $26\times 0{\cdot}2663$, say approximately seven *rattus* to have been caught in the 26 traps. We can apply to these individuals the same arguments used in the case of those rats which collided with traps already occupied by their own species. The proportion of traps unoccupied by *rattus* is $T-n-R/T-n$ and from (6)

$$T\{\log_e(T-n)-\log_e(T-n-R)\}=k'N. \qquad \ldots\ldots(7)$$

It will be seen from the foregoing argument that this equation can hold good only in certain limited conditions. In the first place, the type of trap which is commonly employed as being the most efficient and which can only catch one individual, raises a number of grave difficulties. It might be suggested that it is only when $k'N/T$ is a relatively small quantity, e.g. $<0{\cdot}4$ or $0{\cdot}5$, that it is justifiable to assume the improbability of the individuals who collided with occupied traps, being able to collide with other, unoccupied ones during their remaining search for food. These figures are equivalent to 67–60 % of traps remaining unoccupied and any experiment giving a lower percentage would be suspect. But it is impossible to be dogmatic on this point in the present state of our knowledge and these suggestions must be taken as merely tentative. Lastly the species trapped must be either the only or at least the preponderating type on the area. If the number of traps occupied by other species becomes relatively large, or several species are caught in approximately equal numbers, the conditions are changed and the problem becomes one of the competition for traps between two or more populations, each having different velocities.

5. Arithmetical analysis

The highest value of $k'N/T$ which these results gave was 0·3097 and *R. rattus* was the preponderating type on the area: we shall conclude therefore that a quantity, which was proportional to the population each time the area was trapped, can be calculated by means of the expression

$$T\{\log_e(T-n)-\log_e(T-n-R)\}.$$

It follows that if a suitable function to describe the population can be found, it should be possible to calculate a value for k'. Apart from the loss due to trapping, the population will lose in numbers through the normal death-rate and emigration; and it will gain through immigration from sources outside the area and also the number of young leaving the nest to enter the population at risk. So far as our observations went, the rats of Freetown as a whole showed no violent fluctuations in numbers: it appeared a relatively stable population. Since this experiment lasted for only six weeks, the simplest assumption to make is that during this period immigration and young recruits balanced on the average the loss due to emigration and normal deaths. Then if N_0 be the original number of *rattus* on the area and y the total number trapped up to any particular time t

$$N_t=N_0-y_t,$$

and therefore from (7), putting

$$T\{\log_e(T-n)-\log_e(T-n-R)\}=z, \qquad \text{......(8)}$$

$$z=k'N_0-k'y.$$

That is to say, the values of z should fall on a straight line when plotted against the values of y; $k'N_0$ being the value of z when $y=0$, and k' being the tangent of the angle which the line makes with the y axis. The next step is to fit a straight regression line to the data and to test its goodness of fit by the customary statistical methods. In doing so, we are testing not only whether the assumption of a balanced population is correct, but also the validity of the various assumptions made in section 3. If any one or all of these were to fail, we should expect either that the points of z would fall on a curve relative to the y axis or that no simple functional relationship between z and y could be established.

In calculating the values of z from the observed data by means of equation (8), it is unfortunate, as was mentioned in a previous section, that no figures are available for the number of negative-sprung traps. On another area in Freetown, which was trapped in a similar fashion to the present one, it was observed that in one week during which 630 traps were set overnight, 128 or 20·3 % were found in the morning sprung and containing no rat or other animal. We have assumed this to be an average figure which might be expected in a trapping experiment done under similar urban conditions. The estimate of n for each trapping is thus half the sum of 42 plus the number of traps

observed which were occupied by other species. The estimates of z being made from the proportion of unoccupied traps are subject to large sampling errors (Greenwood & Yule, 1917; Fisher, 1935) and therefore a considerable scatter of the observations will be expected in the graph (see Fig. 3). The sampling variance of an estimate of z is given by

$$\sigma_z^2 = \frac{T^2 R}{(T-n)(T-n-R)},$$

and the square root of this quantity is the standard error. In columns 4 and 5 of Table 3 are given the values of $z \pm$ S.E. derived from the data together with those calculated from the regression line, fitted by the Method of Least Squares,

$$z = 51{\cdot}26737 - 0{\cdot}105642\,y.$$

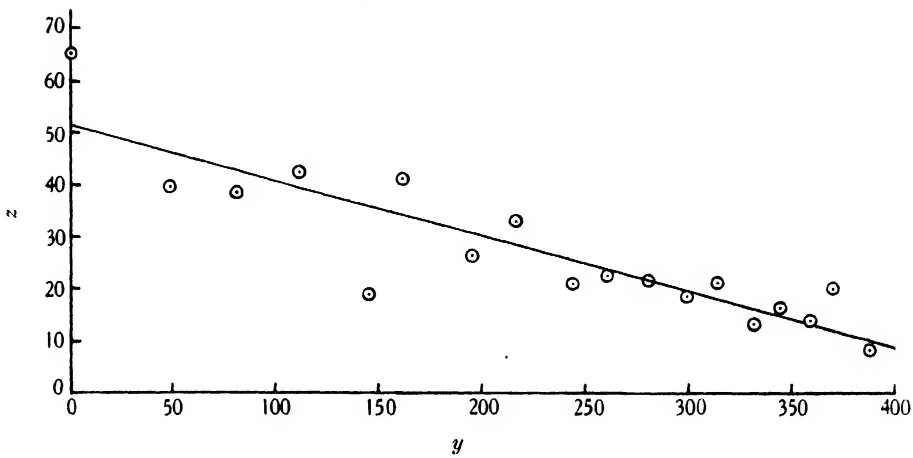


Fig. 3. The observed values of z plotted against y. The equation for the straight line is $z = 51{\cdot}26737 - 0{\cdot}105642\,y$.

The mean sampling variance of the values of z calculated from the observations can be used as a test for the goodness of fit of the regression line, by comparing it with the mean square deviation of the observed values from those calculated by means of the equation. For if the departure from linearity is at all marked, the mean square deviation from the regression line will be significantly greater than the mean variance expected from the errors of random sampling. The mean variance of the 18 values of z is 33·2269 and the sum of the squares of the deviations of the observed values from those calculated by means of the equation, is 735·47669. Since two constants have been calculated from the data, $18-2=16$ degrees of freedom are left and thus the mean square deviation from the regression line is 45·9673. If the estimate of the mean variance of the observed values of z were exact, we could test by means of

$$\frac{\chi^2}{16} = \frac{45{\cdot}9673}{33{\cdot}2269},$$

whence $\chi^2 = 22{\cdot}13.$

Table 3

Trapping no.	$T-n$	y	Observed $z \pm$ S.E.	Calculated z	Expected no. *rattus* trapped	Observed no. *rattus* trapped $=R$
1	184	0	65·03 ± 9·33	51·267	39·9	49
2	185	49	39·88 ± 7·06	46·091	36·5	32
3	183	81	38·98 ± 7·01	42·710	33·7	31
4	185	112	42·65 ± 7·33	39·435	31·7	34
5	184	146	19·10 ± 4·78	35·844	28·9	16
6	185	162	41·26 ± 7·19	34·153	27·8	33
7	186	195	26·43 ± 5·64	30·667	25·3	22
8	184	217	33·32 ± 6·42	28·343	23·2	27
9	181	244	20·71 ± 5·03	25·491	20·7	17
10	187	261	22·50 ± 5·16	23·695	20·0	19
11	182	280	21·87 ± 5·16	21·688	17·9	18
12	185	298	19·00 ± 4·75	19·786	16·6	16
13	187	314	21·25 ± 5·01	18·096	15·4	18
14	188	332	13·85 ± 4·00	16·194	13·9	12
15	186	344	16·43 ± 4·39	14·927	12·8	14
16	186	358	14·01 ± 4·04	13·447	11·5	12
17	187	370	20·02 ± 4·86	12·180	10·5	17
18	185	387	8·10 ± 3·06	10·384	8·9	7
Total					395·2	394

y = Total number of *R. rattus* caught up to the time of each trapping. $\chi^2 = 16{\cdot}792$
$z = 210 \{\log_e (T-n) - \log_e (T-n-R)\}$ $n = 16$
$P = <0{\cdot}50,\ >0{\cdot}30$

For 16 degrees of freedom, $P = <0{\cdot}20,\ >0{\cdot}10$ or in other words a value of χ^2 as large as 22·13 would be expected in about 10 % of such cases. Since the mean variance also has a sampling error, there is really nothing in it and the straight regression line gives a perfectly satisfactory fit to the data.

In columns 6 and 7 of Table 3 are given the observed number of *rattus* caught at each trapping of the area, together with the number expected from theory. These latter figures, allowing for the same number of traps occupied by other species and negatively sprung, are calculated from the values of z in column 5 by means of the expression

$$\text{Expected number of } rattus = (T-n)\,(1-e^{-z/T}).$$

The agreement is very good indeed; $\chi^2 = 16{\cdot}792$ and for 16 degrees of freedom P lies between 0·30–0·50. As judged by these statistical tests, there is nothing in this data which is inconsistent with the various assumptions made during the course of the argument. Whether they are sufficient remains to be seen from further work on the lines indicated in the introduction to this paper.

An estimate can now be made of the two unknown constants, N_0 and $s = cV2r$. The calculated value of $k' = 0{\cdot}105642$; $k'N_0 = 51{\cdot}26737$ and therefore the probable number of *rattus* on the area at the start of the experiment was

$$N_0 = 485.$$

Since $k' = 1 - e^{-k}$, $k = 0{\cdot}111649$; the number of traps set was 210 and since $k = sT$

$$s = 0{\cdot}00053166.$$

As a check on the number of *rattus* which should have been caught during each unit of time, it is now interesting to use equation (4) when $t = 1$, i.e.

$$\frac{T-y}{N-y} = \frac{T}{N} e^{-s(N-T)}.$$

The average number of traps which could catch *rattus* during any particular unit of time, namely $T-n$, is used in this equation instead of the actual number set (T). For the first trapping of the area, $T-n = 184$; inserting this together with the above values of N_0 and s, and solving for y, the expected number of *rattus* $= 40{\cdot}2$. Actually 49 were trapped; so that at the time of the second trapping $N = 485-49 = 436$; $T-n = 185$, whence $y = 36{\cdot}8$. The calculation can be carried out in a similar fashion for the remaining 16 trappings. As shown in Table 3, the expected numbers calculated by the previous method for the first and second trappings were 39·9 and 36·5 respectively, so the agreement is very close indeed.

The last step is to estimate the errors which must be attributed to the calculated values of N_0 and s. If Z be the value calculated by means of the regression line for any particular value of y and z be the observed value, then the mean square deviation from the regression line, n being the number of observations and S the symbol for summation, is

$$\sigma^2 = \frac{S(z-Z)^2}{n-2} = 45{\cdot}967293. \qquad \ldots\ldots(9)$$

Then the variance (V) of k' is given by

$$V(k') = \frac{\sigma^2}{S(y-\bar{y})^2},$$

where $\bar{y}$ is the arithmetic mean of the values of y. The square root of this quantity is the standard error of k' and was found to be 0·014009. Then since

$$1-k' = e^{-k},$$

it can be shown that
$$V(k) = \frac{1}{(1-k')^2} V(k'),$$

whence the standard error of $k = 0{\cdot}015664$. Since $k = sT$ and $T = 210$ is known exactly

$$s = 0{\cdot}00053166 \pm 0{\cdot}00007459.$$

We are greatly indebted to Dr J. O. Irwin for showing us how to arrive at the error of N_0. Write the equation for the straight line in the form of $z = \bar{z} - k'(y-\bar{y})$, where $\bar{z}$ and $\bar{y}$ are the means of the observed values of z and y respectively. Since $k'N_0$ is the value of z when $y = 0$

$$k'N_0 = \bar{z} + k'\bar{y},$$

$$N_0 = \frac{\bar{z}}{k'} + \bar{y}.$$

Whence
$$V(N_0) = V\left(\frac{\bar{z}}{k'}\right) = \frac{V(\bar{z})}{k'^2} + \frac{\bar{z}^2 V(k')}{k'^4}$$

or
$$V(N_0) = \frac{\sigma^2}{k'^2}\left\{\frac{1}{n} + \frac{\bar{z}^2}{k'^2 S(y-\bar{y})^2}\right\},$$

where σ^2 is given by equation (9) above and n is the number of observations (18). Calculating this quantity and taking the square root, we have

$$N_0 = 485 \pm 37.$$

Now we might wish to test whether this estimated number of *rattus* is significantly different from some hypothetical number N'. The hypothesis to be tested is that the deviation $485 - N'$ is distributed normally about zero with a standard deviation of 37, which estimate is based on 16 degrees of freedom. Using "Student's" t test (Fisher, 1935)

$$t = \frac{485 - N'}{37}.$$

From the tables of the distribution of t, for 16 degrees of freedom t has a 5 % chance of lying outside the limits $\pm 2{\cdot}12$. Inserting this value of t in the equation

$$N' = 485 \pm 78.$$

Thus we can say that, assuming the validity of this theory of trapping, the fiducial probability is 95 % that there were between 407 and 563 *R. rattus* on the area at the time when the experiment was started.

6. Discussion

It is an interesting speculation to carry this elementary theory a step further. In the constant $s = cV2r$, the fraction c and the quantity $2r$ refer to the properties of the traps and provided that the type of trap and the method of baiting are unchanged, they can be taken as constant in all such experiments. The quantity V is, however, more complex. We have tended to assume that it is dictated by the food-requirements of the animal. But it is clear that it refers to all the causes of activity on the surface and thus may vary from experiment to experiment, not only with regard to the difficulty of obtaining food at different seasons or on different areas, but also on account of other factors, such as, for instance, the particular species having an increased activity during the mating season. But it is possible to imagine certain conditions, for example a contemporary series of experiments, in which we might feel justified in assuming that V for some particular species could be taken as being approximately of the same relative magnitude on all the areas trapped. Then using the same type of trap and the same unit of trapping time—the latter is a convenience rather than a necessity—and having an estimate of

the value of $cV2r$ from a series of trappings on some unit area, it is theoretically possible to calculate the probable population on another area which has only been trapped once—an immense saving of labour. Any difference in the size of the areas requires an adjustment in the value of $cV2r$, since its essential constituent $V2r$, or the mean area traversed during a unit of time by an individual, is expressed in terms of the unit area. If a_1 be the size of the latter, a_2 the size of any other area and T the number of traps set, then $cV2r\,Ta_1/a_2 = k$: since we have an estimate of the error of $cV2r$, it is therefore possible to find the value of $k' \pm$ S.E. which will apply to the second area. From the proportion of unoccupied traps z is calculated together with its sampling error and z/k' is then the probable population on the area. The error of this estimate, where σ_2 and $\sigma_{k'}$ are the errors of z and k' respectively, is given by

$$\sigma_N = \pm\frac{1}{k'}\sqrt{\left\{\left(\frac{z\sigma_{k'}}{k'}\right)^2+\sigma_z^2\right\}}.$$

These errors are relatively very great: as an example suppose another area, which will be taken as being of the same size as our unit area for the sake of simplicity, had 210 traps set of which 50 were found to have caught *rattus* and $n=0$. Then

$$N=\frac{57{\cdot}1061 \pm 8{\cdot}1009}{0{\cdot}105642 \pm 0{\cdot}014009}$$

$$=541 \pm 105.$$

The percentage error is 19·4 compared with 7·6 which was obtained for the probable population on the unit area: the reason being that the latter is an average figure to the accuracy of which each of the 18 trappings has contributed its quotum of information. In the case of the single trapping, even if k' were known exactly, we would have $N=541 \pm 77$; that is to say, more than two-thirds of the total error is due to the sampling errors involved in an estimate made from the proportion of unoccupied traps. The degree of accuracy which is obtained at any particular level of proportionality, depends on the number of traps set. Suppose that 50 traps had been set on another area and that $a_1/a_2 = 4{\cdot}2$, $n=0$; then k' still has the same value. If 12 *rattus* were trapped—approximately the same proportion of unoccupied traps as in the previous example and also for the first trapping on our unit area—$z=13{\cdot}7218 \pm 3{\cdot}9736$, $N=130 \pm 41$ and the percentage error has risen to 31·5. With increasing proportions of unoccupied traps it rises still higher; for example with 88 % of traps unoccupied and 50 traps set, $z=6{\cdot}3917 \pm 2{\cdot}6112$ and $N=61 \pm 26$ or a 42·6 % error. These considerations affect not only this somewhat speculative application of an estimated value of $cV2r$ to the results from a single trapping, but also the analysis of any experiment designed on the same lines as that in Freetown. If this latter had been carried out on the scale of 50 traps to approximately 5 acres, it is very doubtful whether we

would have been able to establish any agreement between the observed results and those expected from theory.

There is, however, an improvement in the design of such experiments which follows logically from the argument and which would appear well worth the trouble of investigating. In discussing the employment of the single trap we have already touched upon the limitations which this imposes on the values of $k'N/T$. It is true that the latter can always be adjusted to the requisite magnitude either by increasing the number of traps or by leaving them in contact with the population for a shorter period of time. But if, instead of there being one trap at a certain point on the area, a group of three or four traps be set together at the same point, thus forming a trap-unit, many of the difficulties disappear. Theoretically this would permit of a wider range of values for $k'N/T$ giving consistent results, since up to three or four collisions with a trap-unit can now result in capture. Moreover, if the values of $k'N/T$ be such that the probability of there being more collisions than there are traps in the unit is very small indeed, then the conditions symbolized in equation (5) are realised and it follows that the number of animals trapped during a unit of time is proportional to the population or $R = k'N$. The estimate of $k'N$ is now based on a count of a definite number of individuals: a more satisfactory estimate than the less precise one derived from the proportion of unoccupied traps.

Finally it may be suggested that, if the purpose of a trapping experiment be to determine the density of a species at some particular time, it is somewhat unsatisfactory to adopt a method which involves the destruction of a greater part of the population. A system of live-trapping and marking is ecologically much sounder. It is to be hoped that the technique of this type of experiment can be developed along the lines suggested in the preceding paragraph, so that all the effective collisions with a live-trap unit result in capture. Then to take the simplest example of a constant population over the time of the experiment, if every animal captured be marked and released, the total number marked (m) up to the time of any particular trapping is known. Assuming that no deaths occur among the marked individuals and that both marked and unmarked are trapped with equal ease, the number unmarked is $N_0 - m$; then if u be the number of the latter caught at any trapping, $u = k'N_0 - k'm$; and the results are thus susceptible to the same type of arithmetical analysis as used in the present instance. But it is useless entering into details in the absence of any data and this is only a rough sketch of the type of experiment we have in mind. Moreover, further work on this trap-animal reaction may well show that the theory requires a more complicated mathematical treatment than the one employed here as a first approximation.

7. SUMMARY

The results from a series of trappings, all done on the same area in Freetown, Sierra Leone, have been analysed in the light of a theory of trapping, which is merely an adaptation of the elementary kinetic theory of gases. The development of this theory is given in full and the arithmetical analysis of the results has revealed nothing which is inconsistent with the fundamental hypothesis. The probable number of *R. rattus* on this area has been calculated and the errors involved in this type of estimate are discussed, leading to certain suggestions for the design of such experiments in the future.

8. ACKNOWLEDGEMENTS

We are greatly indebted to Mr Charles Elton for his continued interest in this problem and the many stimulating discussions which we had with him over various points. Also to Prof. M. Greenwood, F.R.S., and Dr J. O. Irwin for their kindness in reading the major part of this paper in draft form and for the most valuable criticism and advice which we received from them. The field work was carried out by one of us (D. H. S. D.) under the auspices of the Liverpool School of Tropical Medicine with the permission of the Sierra Leone Government and the co-operation of the Medical Department. The junior author is most grateful to Prof. Warrington Yorke, F.R.S. for the facilities of the Freetown Laboratory and to Dr P. D. Oakley, Director of Medical and Sanitary Services, for the assistance rendered by his Department. He also wishes to express his indebtedness to the Tropical Diseases Committee of the Royal Society for the grant from the Medical Research Fund, which enabled him to carry out his investigations of the rat population of Freetown. Finally he has much pleasure in thanking Profs. R. M. Gordon and T. H. Davey for their suggestions and encouragement during the progress of the investigations.

REFERENCES

Fisher, R. A. (**1935**). "The design of experiments." Edinburgh: Oliver and Boyd.

Greenwood, M. & Yule, G. U. (**1917**). "On the statistical interpretation of some bacteriological methods employed in water analysis." J. Hyg., Camb., 16: 36–54.

Lotka, A. J. (**1925**). "Elements of Physical Biology." Baltimore: Williams and Wilkins.

Petrie, G. F. & Todd, R. E. (**1923**). "A report on plague investigations in Egypt." Rep. Publ. Hlth Labs Cairo, 5: 1–114.

Richter, C. P. (**1927**). "Animal behaviour and internal drives." Q. Rev. Biol. 2: 307–43.

Volterra, V. (**1931**). "Leçons sur la Théorie mathématique de la Lutte pour la Vie." Paris: Gauthier-Villars.

HABITAT SELECTION AMONG BIRDS IN A LAPLAND BIRCH WOOD

By H. N. SOUTHERN and L. S. V. VENABLES

(*With Plates* 4–6)

CONTENTS

		PAGE
1.	Introduction	114
2.	Description of the habitats:	
	(*a*) General considerations	114
	(*b*) The subdivisions of birch forest	115
3.	The avifauna	116
4.	Effect upon commencement of breeding	118
5.	Summary	119
	References	119

1. Introduction

The following notes are a summary of information gathered from field work during two summers in Swedish Lapland. The area worked each time was the basin of the Abiskojokk river, which flows into Lake Torne Träsk near Abisko (Lat. 68° 12′ N., Long. 18° 20′ E.). In neither season were censuses carried out, and the aim of the paper is rather to demonstrate what is the distribution of the bird population in relation to the vegetation of the habitats, and what factors govern the choice of such habitats. It is also proposed to deal briefly with the effect of such habitat selection upon the time of laying of the various species. In 1936 the field work was done during early and mid June by the second author in collaboration with Mr W. H. Thompson; in 1937 from mid June to mid July by the first author in collaboration with Mr W. A. S. Lewis.

We do not propose to restate the theory of habitat selection advanced by Lack (1933), but the field work was done with his ideas in mind, so that it is to a certain extent explanatory of them. Both in the table and in the notes on species it has been assumed that direct limiting factors and indirect ones (via the psychological preferences of the bird) have equal value in determining distribution.

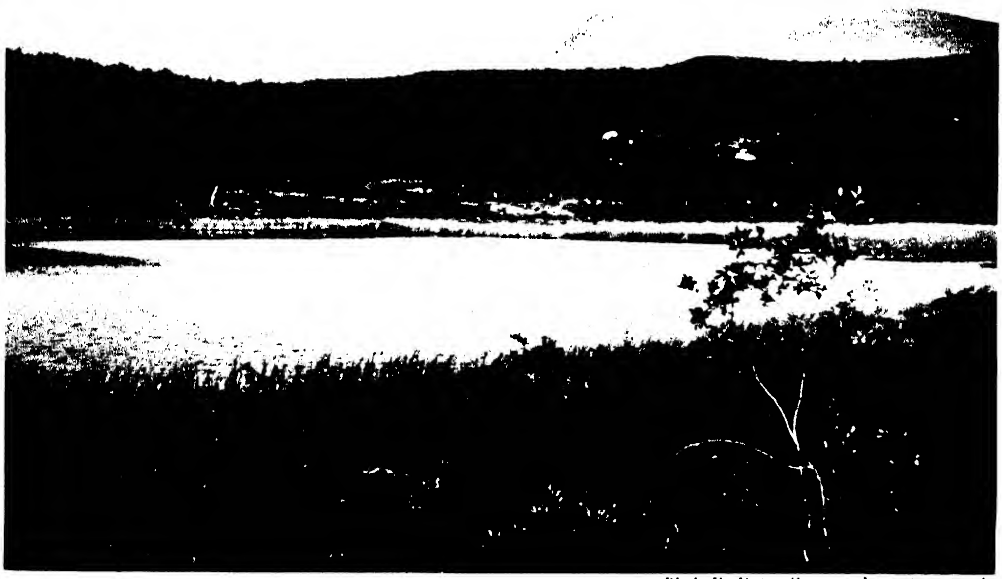
2. Description of the habitats

(*a*) *General considerations*

A brief survey of the major vegetation groups into which this area falls has already been published (Southern & Lewis, 1938). Birch forest (*Betula alba* and many subspecies) occurs in all the river valleys and in this locality

Phot. H. N. Southern and W. A. S. Lewis

Phot. 1. Tributary of the Abiskojokk with silver birch woods on either bank, showing one of the few clumps of conifers.



Phot. H. N. Southern and W. A. S. Lewis

Phot. 2. The three major types of habitat in Swedish Lapland: (1) swamp edge with willow,

extends from 1000 ft. (the height above sea level of Lake Torne Träsk) to about 2500 ft. The tree line is of course much less clearly defined on the more gradual slopes. On the steeper mountain sides there is no dwindling down to scrub, but the last trees are large ones, such as can resist the scouring snow movements, which occur every spring. Thus there is a sharp line marking off the forest avifauna from that of the fells.

The conformation of the land and the snow melt govern the distribution of the major habitats, since, when the latter forms a well-marked canal, which continues to carry down water from the mountains long after the birch woods themselves are clear of snow, the ground remains exceedingly wet; thus a chain of swamps is formed wherever there are slight pockets in the ground and the trees have little chance of spreading in here. Changes of vegetation take place with the alteration of water courses, and in places large numbers of dying birch trees were seen standing in a marshy area, while colonization was taking place in others.

The snow melt is a most important factor in governing the commencement of breeding of birds. Thus hole-nesting species will be able to start much earlier than ground-nesting ones, since the latter must wait not only for the snow melt, but for the drying of the ground. Since this occurs patchily, commencement of breeding is spread over a longer time than with hole or tree nesting species.

(b) *The subdivisions of birch forest*

Roughly these may be given as:

A. Birch forest with good undergrowth.
B. Birch forest with poor undergrowth.
C. Birch scrub with good undergrowth.
D. Birch scrub with poor undergrowth.
E. Swamp edge.

Type A of course contains the largest trees of all, and in this habitat come the small clumps of conifers (*Pinus sylvestris* var. *lapponica*) which crop up only occasionally as far north as this. The effect upon the avifauna however is noticeable. All the larger birds nest in these for preference, e.g. hooded crows, merlins, ospreys (*Pandion haliaetus*), rough-legged buzzards (though most of these last are out on the fells), and even fieldfares and bullfinches (*Pyrrhula p. pyrrhula*). In addition a pair of non-breeding waxwings (*Bombycilla garrulus*) was seen in 1936 in the conifer areas. The earlier party also saw old nesting sites of black woodpeckers (*Dryocopus martius*), which are probably limited to these trees, since no birch would be large enough to accommodate them.

Much of the birch forest of types A and B was closed, though large areas of open formation were present, these being inhabited especially by flycatchers and redstarts. Some parts naturally were intermediate between the two types. Other trees also occurred, such as bird cherry (*Prunus padus*), some Salices

(though these were mostly in the swamps), and some poplars (*Populus*). These however could have had little effect upon the bird distribution. The birches in A and B were mostly about 20–25 ft. high, though 30 ft. was not an uncommon size; in C and D the scrub was generally dense and ranged up to 12 ft. in height with isolated larger trees in places.

In A and C the secondary growth was remarkably dense and the following plants were co-dominant: *Empetrum nigrum*, *Vaccinium vitis-idaea*, *Juniperus communis var. nana*, *Phyllodoce coerulea*, *Cassiope tetragona* and *Betula nana*. In B and D much the same plants were present but the dryness of the ground made them much sparser. Most of the vegetation occurs upon fairly dry ground, off which the snow melt drains early. In wetter parts swamp vegetation appears; *Trollius europaeus*, *Viola biflora*, etc., and the type of habitat may be then classed as verging towards E.

Exposure is also a factor to be reckoned with: most of the lakeside conformed to type A, but one headland, which was very windswept, approximated more to type C. On the whole, however, the dampness of the ground was the chief determining factor.

3. The avifauna

The distribution of the various species is given in the table. The following notes on some of them are appended.

(1) *Brambling*, *mealy redpoll* and *willow warbler*. These three species may be reckoned as the most adaptable since two of them are found in all five habitats and the third in all but swamp edge. The mealy redpoll and willow warbler even extend into areas up on the fells which cannot even be classed as scrub, the former nesting, when necessary, on the ground, the latter occupying any small clump of bushes, provided that a song-post 6–8 ft. high is present. This limitation in the willow warbler's case is again seen in type E habitat, where it will nest away from the trees in clumps among the marshes, but still sings from the nearest forest edge. It is even able to overcome nesting difficulties presented by lack of undergrowth, and in 1937 two nests were discovered built quite openly of conspicuous grasses in 3 in. *Vaccinium*.

(2) *Woodpeckers* and *tits*. The former are only found in types A and C, because they are unable to adapt themselves to the small trunks of the birches in scrub areas. Willow tits inhabit chiefly swamp edges and the damper parts of A, because they must have decaying trees in which the excavation of nest holes is easy.

(3) *Fieldfare* and *redwing*. These are also confined to A and B by nesting requirements and also by the necessity for a song-post. The redwing may nest on the ground and still need a tree from which to sing. The fieldfare is much more a colonial nester and new nests are generally found close to those of the previous year, which last very well, since they are constructed of mud and kept in cold storage all winter.

Phot. H. N. Southern

Redwing (*Turdus musicus*) nesting on the ground. The ground vegetation is typical of fairly open birch wood, consisting largely of *Vaccinium* and *Empetrum*.

Distribution of birds in subarctic birch wood

A = wood with good undergrowth. C = scrub with good undergrowth.
B = wood with poor undergrowth. D = scrub with poor undergrowth.
E = swamp edge.

Species	A	B	C	D	E	Special features	Date of first egg
Hooded crow (*Corvus c. cornix*)	×	×	.	.	.	Tall tree for nesting	May
Magpie (*Pica p. pica*)	×	×	.	.	.		May
Mealy redpoll (*Carduelis f. flammea*	×	×	×	×	×	Nest in fork at any height or even built on the ground. *Salix* fluff for nest material	24 July
Pine grosbeak (*Pinicola e. enucleator*)	×	×	.	.	.	—	—
Brambling (*Fringilla montifringilla*)	×	×	×	×	.	Nest in fork at any height, but generally high	10 June–1 July
N. willow tit (*Parus atricapillus borealis*)	×	×	.	.	×	Large stump for nesting. Most at or near marsh	28 May
Spotted flycatcher (*Muscicapa s. striata*)	×	×	.	.	.	Open formation for "snapping" method of feeding. Nest often in broken-off birch stump	14 June
Pied flycatcher (*Muscicapa h. hypoleuca*)	×	×	.	.	.	Open formation or wood edge for "pouncing" method of feeding. Song-post. Nest holes not in C and D	12 June
N. willow warbler (*Phylloscopus trochilus acredula*)	×	×	×	×	×	Some undergrowth under which to conceal nest. Song-post. Usually least common in D on account of exposure	14–25 June
Garden warbler (*Sylvia borin*)	×	.	×	.	.	Tall, dense undergrowth for nesting	Arrival 25 June
Redwing (*Turdus musicus*)	×	×	.	.	.	Tall song-post. If a ground nester, some undergrowth in which to conceal nest	20 May and 23 June
Fieldfare (*Turdus pilaris*)	×	×	.	.	.	Tall song-post. Fork for nest at any height	28 May and 1 July
Redstart (*Phoenicurus p. phoenicurus*)	×	×	.	.	.	Same as for pied flycatcher	12 June
Arctic bluethroat (*Luscinia suecica*)	×	.	×	.	×	Confined to formations with undergrowth for nesting place	8 June
Dunnock (*Prunella m. modularis*)	×	.	.	.	.	Tall, dense undergrowth for nesting	—
Three-toed woodpecker (*Picoides tridactylus*)	×	×	.	.	.	Open formation where the largest trunks are	17 May
N. lesser spotted woodpecker (*Dryobates m. minor*)	×	×	.	.	.		18 May
Merlin (*Falco columbarius aesalon*)	×	×	.	.	.	Tall tree for nesting	June
Rough-legged buzzard (*Buteo l. lagopus*)	×	.	.	.	.		16 May
Willow grouse (*Lagopus l. lagopus*)	×	.	×	.	.	Undergrowth for nesting.	3–10 June
Total species	20	15	6	3	4		

(4) *Garden warbler* and *dunnock.* Both these species are uncommon and only found in the densest parts of habitat A. Thus they are among the least adaptable of the birch wood birds.

(5) *Bluethroat.* This species shows a marked preference for type C and will sing from almost any height, so long as it is sufficiently conspicuous. Along the railway a favourite song-post was on the electric cables. Nesting limitations confine it to areas with good undergrowth.

(6) *Flycatchers* and *redstart.* These are subject to roughly the same nesting limitations as the woodpeckers, but their mode of feeding further confines them to places where the formation is open. Song is uttered from among the trees and not necessarily from conspicuous branches, though no doubt scrub would be too dense for this purpose.

In general it may be seen that the birds may be classified in this way according to their adaptability. Thus the most adaptable may be said to be the commonest species, and the fall-off in the number of habitats occupied is generally accompanied by a decline in absolute numbers of the birds. Exceptions to this are the woodpeckers, which are not at all common, while the bluethroat is locally very abundant, when the type of ground is suitable. However, the numbers and ubiquity of such species as mealy redpoll and brambling are remarkable.

4. Effect upon commencement of breeding

The dates given in the right-hand column of the table are all taken from 1937, when considerably more nests were found. In many cases they are approximate, having been worked out from the time of hatching or fledging, but it is probable that they are correct enough to a few days. It should be pointed out that the spring in 1937 was an exceptionally early one, so that the dates are only valuable relatively to one another. Two points should especially be noticed.

(1) The habitat selection of the bird largely determines the extent to which the onset of breeding is affected by the snow melt. Thus all the species that nest in trees, either in the branches or in holes, can start considerably earlier than ground nesters. Woodpeckers, tits and the larger tree-nesting species, such as the rough-legged buzzard, hooded crow and magpie, all started about the middle of May, and they are followed shortly towards the end of the month by the fieldfares and redwings. In early June these are followed by other tree-nesters, such as the brambling and redstart. Of those which lag behind the mealy redpoll seems to be limited by a supply of *Salix* fluff, with which the nest is invariably lined. This may not be quite such an arbitrary habit as it sounds, since the white colour of the nest lining may counteract the ill effects of excessive heat upon the nestlings and influence chick mortality, as Linsdale (1936) found in the case of some American birds. The flycatchers are noticeably

Phot. H. N. Southern

Phot. 1. Three-toed woodpecker, ♀ (*Picoides tridactylus*), one of the early nesters, using the larger birches for nesting sites.

Phot. H. N. Southern

Phot. 2. Mealy redpoll, ♀ (*Carduelis f. flammea*), a late nester, using birches of all sizes.

***Face page* 118**

late arrivals in Britain, and this lateness may be correlated with the amount of insect prey upon the wing.

The earliest of the ground nesters are the bluethroat and the willow grouse and they are probably inclined to occupy the areas of wood that dry up first. After these comes the willow warbler, and the series can be continued by including the swamp nesters, all of which are comparatively late.

(2) Among the species which are directly influenced in nesting by the state of the ground, considerable variation in the date of breeding onset is noted. This is no doubt correlated with the different speeds at which areas dry off after the snow melt. Lack (1933) found a similar case in the Arctic terns (*Sterna macrura*) on Bear Island. Both willow warbler and willow grouse show this variation, though it is only fair to add that so does the brambling. Further evidence is again shown by swamp and fell species; meadow pipit (*Anthus pratensis*) nests were found in 1937 in all possible stages, while the same applied in a less degree to reed bunting (*Emberiza s. schoeniclus*) wheatear (*Oenanthe oe. oenanthe*) and snow bunting (*Plectrophenax nivalis*).

In conclusion the authors wish to point out that although the last part of this paper is considered most suggestive, it would be much strengthened by any further data that future workers in this area may obtain.

5. Summary

1. Observations on the habitat selection of birds in a subarctic birch wood were made in 1936 and 1937.

2. The major habitats are defined and the subdivisions of birch wood indicated.

3. The types of habitat favoured by each species are given and the limiting factors noted.

4. From these data it is shown that, roughly speaking, the most adaptable species are the commonest.

5. Dates of the onset of breeding are correlated with the type of habitat, through the influence on the latter of the date of snow melting.

6. Ground nesters therefore show more variation in this date, since the ground dries unevenly.

REFERENCES

Lack, D. (1933). "Habitat selection in birds." J. Anim. Ecol. 2: 239–62.

Southern, H. N. & Lewis, W. A. S. (1938). "Infra-red photograph of Arctic birch forest and fells." J. Ecol. 26: 328–30.

Linsdale, J. M. (1936). "Coloration of downy young birds and of nest linings." Condor, 38: 111–17.

Lack, D. (1933). "Nesting conditions as a factor controlling breeding time in birds." Proc. Zool. Soc. Lond.: 231–7.

STUDIES OF THE SOIL FAUNA, WITH SPECIAL REFERENCE TO THE RECOLONIZATION OF STERILIZED SOIL

By K. D. BAWEJA

Rothamsted Experimental Station, Harpenden

(*With Plate* 7 *and* 12 *Figures in the Text*)

CONTENTS

		PAGE
1.	Introduction	121
2.	Review of previous work	121
3.	Lay-out of the experiment: Allotment area	123
4.	Soil analysis	125
5.	Survey of the flora	125
6.	Sterilization of experimental plots	126
7.	Technique	128
	(*a*) Sampling	128
	(*b*) Rearing	129
	(*c*) Preservation of material	130
8.	Effect of the hawthorn hedge on the soil population	130
9.	Composition of the soil fauna:	
	(*a*) General comparison	131
	(*b*) Controls	132
	(*c*) Sterilized plots	134
10.	Normal seasonal changes	137
	(*a*) Unenclosed controls	137
	(*b*) Enclosed controls	145
	(*c*) Effect of atmospheric and soil temperatures on the activity of soil organisms	146
11.	Rate of recolonization of the sterilized plots:	
	(*a*) Unenclosed plots	147
	(*b*) Enclosed plots	149
	(*c*) Comparison of the total population of simultaneous sterilizations	
	(1) Sterilization 1	150
	(2) Sterilization 2	150
12.	Behaviour of some population components	152
13.	Economic aspect	154
14.	Comparison of enclosed and unenclosed plots	155
15.	Subsoil population	157
16.	Acknowledgements	159
17.	Summary	159
	References	161

1. Introduction

The present investigation was designed primarily to supply information on the recolonization of sterilized soil by soil macro-organisms. Soil sterilization is commonly practised in glasshouse horticulture for restoring the fertility of the soil and the destruction of the noxious animals; but a perusal of the literature revealed the fact that no evidence was available concerning the recolonization of the sterilized soil by such animals.

The work was undertaken at the suggestion of Dr C. B. Williams and was carried out from November 1935 to March 1937 at Rothamsted Experimental Station, Harpenden.

Advantage was taken of the fact that a new machine for isolating soil fauna had been recently designed by Ladell (1936). This apparatus, by means of which the fauna is floated out of the soil, has been used throughout the investigation.

The term soil fauna is used to include all the macro-organisms which at one time or the other in the course of their development from egg to the adult stage, spend a part or whole of their life time beneath the surface of the soil. According to this definition they may be permanent denizens of the soil or temporary visitors for the purpose of food, shelter, etc.

2. Review of previous work

The earliest attempt to study the soil fauna was in Europe by Diem (1903), followed by Holdaus (1910) who published brief records of the soil organisms. American zoologists followed suit and took up the study of the ecological relationship of insects and other invertebrates. McAtee (1907) made a preliminary start by examining an area of 4 sq. ft. of the forest floor and the grassy meadow at Washington for insects and seeds in order to study their relationship to the bird food. He computed 1·2 million invertebrates per acre for the former and 13·7 million for the latter habitat. Comprehensive insect surveys were soon after organized to preserve for the future a record of the fauna of some of the American States in transformation from wilderness to agricultural and industrial countries. The work of Shelford (1913), Vestal (1913) and Adams (1915) is of great significance in this connexion.

More intensive types of investigations were also undertaken at this time in England and some useful information obtained. It was found that, owing to the continuous changes brought about by cultivation, soil insects were not homogeneous in distribution except to some slight extent in grassland, but that even there the composition was considerably affected by the migration of the insects to and from the arable lands. The first soil insect survey was carried out by Cameron (1913) at Manchester, where he recorded 163 species, the majority of them surface forms. He dealt with an area which was not uniform and possessed heterogeneous vegetation. His second paper (1917) deals with similar investigations of two types of grassland in Cheshire. The difference in

fauna which he observed in these areas was attributed to the different environmental conditions. Buckle (1921) working at the same place concluded a little later that the distribution and numbers of the soil fauna were more stable on grassland than on arable land; that the fauna increased in both with the growth of vegetation, and that there was no characteristic fauna of arable land. Morris (1920) made a study of a permanent pasture, also in Cheshire, and estimated a population of 3·6 millions per acre, Coleoptera predominating in number of species. He also found that the factors influencing the depth distribution were chiefly food, aeration and moisture. His second paper (1922) describes the effect of farm manure on arable land at Rothamsted. He observed that the application of the farmyard manure increased the invertebrate population, but that the latter were predominantly saprophagous and not injurious to growing crops. He studied the depth of soil fauna also and concluded that the greatest number of insects and other invertebrates was confined to the upper 3 in. of the soil, though some species penetrated to a greater depth. He also attempted an estimate of nitrogen contained in the bodies of the soil fauna and found that there was no likelihood of any appreciable loss of nitrogen from the soil due to migration of the winged members of the fauna. In his third paper (1927) he gives an account of the effect of artificial manures on a soil population observed a little later in the same locality. He concluded that although artificial manures had little or no effect on the soil fauna, the effect of dung in increasing the number and the number of species was considerable.

Thompson (1924) examined an area at Aberystwyth, chiefly under grass, but with some cultivated land. The qualitative and quantitative seasonal variations observed by her were correlated with the general environmental conditions. She also found that Collembola and Acarina were markedly the dominant groups, and that the maximum population occurred during winter months, owing to relative absence of drought conditions. Edwards (1929) followed with an investigation of the insect fauna of four distinct types of soil from a permanent pasture and one from an arable land, also at Aberystwyth. He noticed that the components of the fauna differed in relation to different soil types and also attempted to correlate them with environmental conditions. He also observed that the injurious insects occurred in all four pastures with some slight variations in density.

Ford (1935) made an investigation of the animal population of soil and vegetation of the ridges transversing a meadow at certain favourable times of the year, and obtained a total density of 263·8 million individuals per acre in the soil and 8·8 million in the surface vegetation. He also observed that the greatest concentration existed between 1 to 1·5 in. below surface, few organisms below 4·5 in. and none below 8 in.; that the winter months showed a rising population to December and a falling one from January to May; and that the fluctuations were confined entirely to Collembola.

Ingram (1931) carried out a survey of the sugar-cane fields in Louisiana and showed the number of soil animals and root injury to be greatest in heavy soils. The most numerous of the injurious species were a Symphylid, *Hanseniella unguiculata*, springtails, *Lepidocyrtus violentus* and *Onychiurus armatus*, a bristle-tail, *Japyx* sp., and a snail, *Zonitoides arboreus*, their average population amounting to 10·5 million per acre. He also determined the length of time required for these soil animals to reach normal population following what he calls "extermination by flooding" and remarked: "It appears that if injurious soil animals were destroyed, benefit would be derived the year following, but the second year the soil animal population would have reached normal numbers again."

Frenzel (1936) made a comparative study of the soil fauna of some different habitats situated at elevations varying from 110 to 2000 m. in Germany and concluded that soil moisture depending upon soil structure was most important in influencing the population. He also pointed out the ecological plasticity of some of the soil organisms. In all he recorded 422 species from these habitats, with a minimum of 68 and maximum of 203 species per habitat. Peak period of the soil population in his observations occurred during October and again in early spring, and the minimum population in midwinter and midsummer.

The study of the soil fauna, as the above brief account will show, had so far been confined to the analysis of their density in relation to the environmental factors, and no qualitative data on recolonization had ever been collected.

3. LAY-OUT OF THE EXPERIMENT

Allotment area

The Rothamsted Experimental Station at Harpenden is situated 25 miles north of London, at an elevation of about 400 ft. above sea-level. A small piece of land on the allotments situated in the neighbourhood of the Insectary was selected. This was bounded by a hawthorn (*Crataegus oxyacantha*) hedge about 10 ft. high on the north, by the site of a bonfire on the east and by vegetable gardens on the south and west. As the land had been uncultivated for a period of two years, it had developed a thick cover of vegetation. The latter was cleared by cultivating the entire area to a depth of 1 ft. at the end of November 1935. No further steps were taken for a month, in order to enable the soil to regain its normal activities.

Twelve plots, each 9 ft. square, were next marked out in two equal sets. One set (series A) was kept unenclosed and a margin of at least 1 ft. allowed between individual plots. Each plot in the second set (series B) was enclosed by iron sheets fixed 1 ft. below the ground and extending 6 in. above the surface. Pl. 7 shows the lay-out of the experiment at the time of first sterilization. Each set was made up of two rows each with three plots in a line. One control was allowed for every two treated plots, so that ultimately there were two sterilized

plots together with one control in each row. The selection of the plots was arrived at by a random method. The entire design of the experiment is shown in Fig. 1. The arrangement of the plots may be summarized as follows:

Series A, Unenclosed
- Sterilization I (February)
  - Plot A 01 — Control
  - Plots A 1 and A 2 — Sterilized
- Sterilization II (May)
  - Plot A 02 — Control
  - Plots A 3 and A 4 — Sterilized

Series B, Enclosed
- Sterilization I (February)
  - Plot B 01 — Control
  - Plots B 1 and B 2 — Sterilized
- Sterilization II (May)
  - Plot B 02 — Control
  - Plots B 3 and B 4 — Sterilized

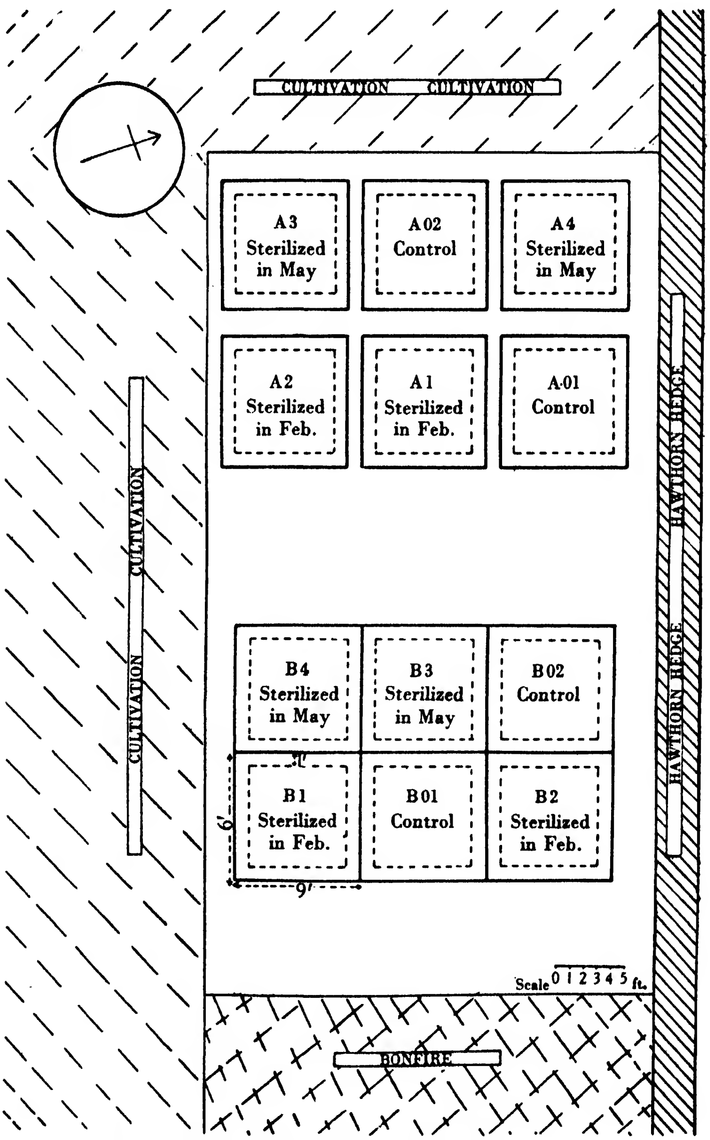
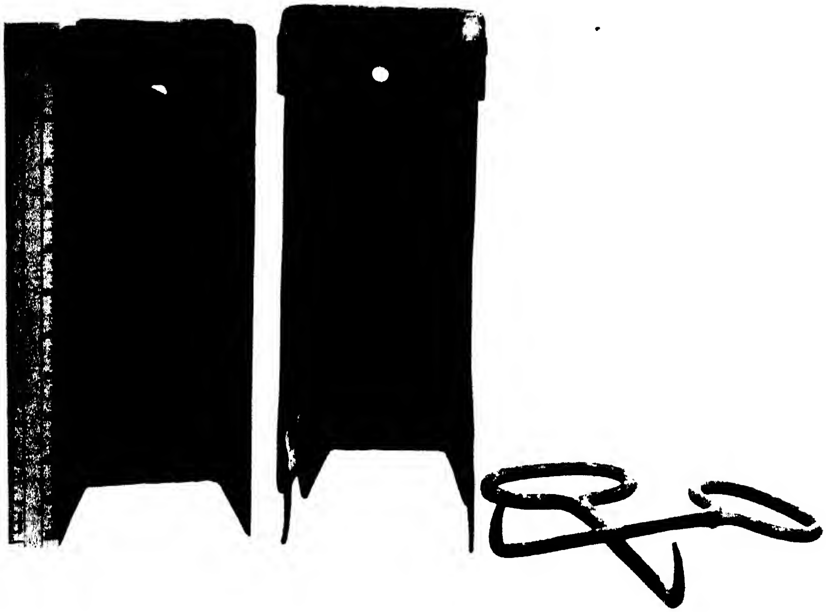


Fig. 1. Design of experiment, allotment area.

(c)



(b)

(a)

With the exception of the controls, the soil of all the plots was sterilized by removing it to an oven and baking it to 212° F.; the experiment was divided into two parts as explained later. Observations on all the control plots were undertaken from January 1936 and on the treated plots immediately after they were sterilized. A margin of 1 ft. was allowed inside the plots so that the actual examination of the soil fauna was made on 7×7 sq. ft.

In addition to the above, observations were also carried out on the arable as well as on the permanent pasture for purpose of comparison. These results are not included in the present paper.

4. Soil analysis

The soil of Rothamsted fields is sticky clay with a considerable amount of flints in it, overlying chalk. Mechanical analysis of all the different types of soil examined was done by the Physics Department at Rothamsted Experimental Station to whom I am indebted.

	Allotment area	
	Unenclosed %	Enclosed %
Coarse sand	11·6	10·6
Fine sand	35·5	36·5
Silt	20·0	21·5
Clay	17·5	17·5
Carbonates	—	—
Air dry moisture	3·1	2·9
Loss by solution	1·2	1·0
Loss by ignition	9·9	9·8

5. Survey of the flora

A floral survey was carried out before disturbing the soil of the allotment area. One square foot of the ground was taken at random and all the plants counted. A number of such observations were made and the density of the vegetation observed. I am grateful to Dr Winifred E. Brenchley, Rothamsted Experimental Station, who very kindly identified these plants for me.

Name of plant	Density %
1. *Poa annua* L.	41·3
2. *Galium Aparine* L.	29·4
3. *Senecio vulgaris* L.	11·4
4. *Ranunculus repens* L.	7·3
5. *Sonchus oleraceus* L.	2·9
6. *Plantago lanceolata* L.	1·3
7. Others: *Medicago lupulina* L., *Anagallis arvensis* L., *Papaver Rhoeas* L., *Daucus Carota* L., *Carum Petroselinum* B & H.F., *Sonchus* sp., *Capsella Bursa-pastoris* Moen., *Lamium album* L., and *Veronica Buxbaumii* Ten.	4·4

Throughout spring and summer weeds continued to grow in close vicinity of the plots and were removed as frequently as possible to avoid their interference with the experiment. Some stray specimens of *Euphorbia*

Helioscopia L., *Veronica Buxbaumii*, *Senecio vulgaris* and *Capsella Bursa-pastoris* were at times observed in the sterilized plots and removed. Weeding of the control plots was carried out a number of times, but the following survived in small numbers: *Matricaria inodora* L., *Anagallis arvensis*, *Convolvulus arvensis* L., *Medicago lupulina*, *Lapsana communis* L., *Lamium purpureum* L., *Euphorbia Helioscopia*, *Veronica Buxbaumii*, *Capsella Bursa-pastoris*, *Sonchus oleraceus* L., *Papaver Rhoeas* and *Plantago lanceolata*.

6. Sterilization of experimental plots

Sterilization of the soil is carried out in two ways: (*a*) by use of chemicals, (*b*) by application of heat.

(*a*) *Use of chemicals*

Chemicals are mostly employed in moderate doses for the partial sterilization of soil or for the eradication of a particular type of harmful soil organism, but in the present case complete extinction of all kinds of macro-organisms was intended and, therefore, the treatment had to be more drastic. A number of chemicals were considered: cresylic acid, carbon bisulphide, potassium cyanide, ethylene oxide, etc.; but as it was necessary that the chemical selected should possess quick toxic effect on the soil organisms and leave no residue behind, carbon bisulphide was preferred. Preliminary observations were carried out in four small plots (1 × 1 yard) enclosed by means of iron sheets to a depth of 1 ft., one of them having been set aside as control and the remaining three subjected to various treatments (Pl. 7*a*). Varying doses of the fumigant were tried. The plot receiving 2, 4 and 8 oz. per sq. ft. in the first treatment was given another dose of 14, 12 and 8 oz. respectively in the second. The percentage of destruction in the case of heavy doses amounted only to 95. The toxic effect was weak in action on account of the excessive soil moisture resulting from the continuous wet weather slowing down the diffusion of the carbon bisulphide. Use of still higher doses, besides being uncertain in effect, was very expensive, and this method of sterilization had to be abandoned in favour of a more satisfactory one.

(*b*) *Application of heat*

Different methods of applying heat to the soil for sterilization purposes are in vogue in England. The original idea was to sterilize the soil *in situ* so as to disturb its texture as little as possible, but the enquiries conducted for this purpose soon revealed the impractibility of the idea owing to heavy expenses involved in erecting the elaborate outfit necessary for the operation.

Baking, which is regarded as equally effective (Bewley, 1929), was resorted to. Messrs H. B. Randell, Ox Lane Nurseries, Harpenden, who possessed a "Vulcano" sterilizer (Holmes Patent No. 2057), were entrusted with the task,

and the treatment of the plots was carried out by them in a most satisfactory manner. The soil of the experimental plots was dug to a depth of 1 ft. and carted to the nursery. The temperature of the kiln was raised gradually to 212° F. and maintained for 6 hr. After treatment the soil was carted back to its respective plots. The different treatments were carried out as given below:

Sterilization 1

Plots A 1 and A 2 Unenclosed Plots B 1 and B 2 Enclosed	Sterilized between 14 Feb. and 2 March 1936

Sterilization 2

Plots A 3 and A 4 Unenclosed Plots B 3 and B 4 Enclosed	Sterilized between 6 and 28 May 1936

Before disturbing the soil for sterilization, samples were taken in order to ascertain the soil population, and the same process was repeated after it was brought back and packed into its proper position. In no instance was any living organism discovered in the baked soil, so that the recolonization of the treated plots actually started from a stage of completely eradicated macro-organic life down to a depth of 12 in.

Subsequent treatments of plots

A sample of the sterilized soil was sent for chemical analysis, and it was seen that the mineral nitrogen had considerably increased, as had been anticipated (Table 1). The chemical analysis was done by the Chemical Department of Rothamsted Experimental Station, Harpenden, to the members of which I am grateful.

Table 1. *Increase of mineral nitrogen in the sterilized plots. Mineral nitrogen mg./g.*

Plot	Before sterilization (*a*)	After sterilization (*b*)	Difference (*b* − *a*)
Sterilization 1, unenclosed plots	12·1	95	+82·9
Sterilization 1, enclosed plots	8·6	90·6	+82
Sterilization 2, unenclosed plots	13·5	62·1	+48·6
Sterilization 2, enclosed plots	11·2	73·0	+61·8

The vast increase of mineral nitrogen in the sterilized plots was due mainly to the breakdown of the organic matter forming ammonia. The sterilization had the effect of destroying the nitrifying organisms, the ammonia therefore remaining as such. In order to restore the phosphorus-nitrogen ratio, a dressing of superphosphate was given to each plot, including the controls, at the rate of 1·1 oz. per sq. yard, immediately after sterilization.

To provide some food to the recolonizating organisms, it was deemed necessary to grow some kind of crop on the plots. Various food plants will support different faunas, and after some consideration a lawn grass-seed mixture, in which rye grass (*Lolium perenne*) predominated, was selected and

raked in at the rate of 1·2 oz. per sq. yard. Germination started after about 3 weeks. The growth was very vigorous in the sterilized plots, and since it soon began interfering with the sampling process, the grass had to be mowed at regular intervals. Four such mowings were done in the sterilized plots, whereas one alone sufficed on the controls.

The grass on the sterilized plots was thicker in texture, of healthier appearance and much darker in colour than that of the controls. Pl. 7 (*b*) shows the plots at the end of the observations. The difference in growth is perceptible even after a lapse of one year. The profuse growth was evidently the outcome of sterilization and it had a marked effect on the rate of recolonization of the soil organisms.

7. Technique

The Ladell apparatus (1936) was employed throughout the investigation, after it had been subjected to certain tests. The principle involved in the apparatus is flotation in a dense stratum aided by stirring the soil and bubbling a fine stream of air from below. Magnesium sulphate solution with a specific gravity of 1·11 was used. This method, besides being efficient and accurate, possesses many advantages over the previous ones, the chief being rapidity, non-toxicity and cleanliness.

(*a*) *Sampling*

One sample from the control and one from the corresponding sterilized plots of each of the unenclosed and enclosed areas were examined during each week. With this plan it was possible to examine each control twice, and the sterilized once in 4 weeks (for ease of description termed "month").

One sample could be examined in a day except during the peak period when it took a little longer. In such instances, the debris was preserved in alcohol and examined during leisure hours. During the period of the entire investigation from November 1935 to March 1937, a total of 214 samples was examined, excluding 86 which were taken from the arable and pasture lands and from other places for miscellaneous observations.

This sampling was made possible by the speed and efficiency of the Ladell's apparatus. No such previous investigations were ever extended to such a large number of samples, as will be seen from the following comparison:

Table 2. *Comparison of soil samples examined in present and past investigations*

Reference	Locality	Size of sample in.	No. of samples examined
Morris (1920)	Cheshire	10 × 10 × 24	29
Morris (1922)	Rothamsted	9 × 9 × 9	46
Morris (1927)	Rothamsted	9 × 9 × 9	45
Thompson (1924)	Aberystwyth	9 × 9 × 9	34
Edwards (1929)	Aberystwyth	9 × 9 × 9	20
Ford (1935)	Oxford	3 × 3 × 9	28
Present investigations	Rothamsted	3 × 4 × 9	300

The soil samples were taken by means of a specially designed tool (Pl. 7*c*). It was made up of iron plate 3 mm. in thickness bent to form three sides of an open rectangular chamber measuring 3×4 in. at the top and 12 in. deep. The open sides of the chamber were covered separately by iron plate of corresponding thickness and length. The lower ends of the chamber, as well as the plate, were cut out to form strong projecting teeth $1\frac{1}{4}$ in. in length and sharpened for rapid penetration into the soil. An iron plate $1\frac{1}{4}$ in. wide was fastened at the top of the chamber and the plate, with a hole below on each side for withdrawing the tool by means of iron hooks from the soil. The sampler measured 9 in. from the holes to the base of the teeth, so that when driven completely into the soil it cut a block of $3 \times 4 \times 9$ in. This was the size of the sample used throughout the experiment.

The exact position of the sample was determined by randomization. The spot was cleared of the vegetation by cutting it with a pair of scissors very close to the surface in order to exclude all above-ground forms. The sampler was then hammered into the soil and the block pulled out. The soil was transferred to a cloth bag and brought to the laboratory for further treatment. In the majority of cases it came out in a compact form, but in some instances the lower part crumbled and was gathered by hand. Each time before leaving the plot the dimension of the hole was checked by a foot rule.

The isolation of the soil fauna was carried out in the manner described by Ladell (1936), with certain modifications.

(*b*) *Rearing*

In almost all the samples which were examined, immature forms of various types were present. The majority of them were difficult to identify and had to be bred for further study. Their breeding was rendered difficult on account of the scanty numbers in which many of them occurred. As the investigation progressed their variety increased and the rearing, therefore, became more and more important. In all, 30 species of Diptera, 19 of parasitic Hymenoptera, one of Lepidoptera, and one of Orthoptera were bred from either the larval or the pupal stage to the adult. In addition, eggs were also recovered every now and again and had to be incubated for accurate information. Eggs of *Campodea* (Thysanura); *Forficula auricularia* L. (Dermaptera); *Harpalus*, *Amara*, *Tachyporus*, *Quedius*, *Philonthus*, *Staphylinus*, *Lacon*, *Chaetocnema* (Coleoptera); *Acocephalus* and *Nabis* (Hemiptera); *Agrotis* and two undetermined spp. (Lepidoptera); one undetermined sp. probably *Lithobius* (Myriopoda); two undetermined spp. of Araneida (Spider); and *Arion* (Gastropoda) were thus determined.

(c) *Preservation of material*

Insects which could not be pinned or mounted properly were preserved in 70% alcohol. Special treatment was necessary for the detailed study of the following:

Collembola. Air bubbles which always adhered to the body of the Collembola interfered with counting. Handschin (1929) recommends the use of a few drops of chloroform to overcome this trouble, but it was not found satisfactory. Immersion of the tube containing the specimens in water-bath (95° F.) for a minute or so followed by gentle shaking, proved quite useful. Besides, the heat served to stretch the insects, facilitating their quick provisional determination. For more detailed study, mounts were made in Berlese fluid.

Larvae. Larvae were killed in boiling water. This process, though it slightly extended their bodies, possessed the advantage, especially in Diptera, of retaining their colour which in alcohol generally turned greyish black otherwise.

Acarina. They were cleared in Koenike's fluid for a few days before mounting.

8. Effect of the hawthorn hedge on the soil population

The hawthorn hedge (Fig. 1), which formed a barrier on the north about 3 ft. away from the experimental plots of the allotment area, might have been expected to have an influence on the density of the soil organisms in its neighbourhood. In the course of investigations it became apparent that some observations were essential to elucidate this point. The narrow strip lying between the plots and the hedge was examined at different positions in April 1936. The relationship of population of the strip and the adjoining controls at the corresponding periods is worked out below:

Soil population per sample

Narrow strip	Control	Increase
105	46	×2·3
251	169·5*	×1·5
143	68·5*	×2·1

* Mean of two observations.

The population in the strip proved 1·5–2·3 times higher than the controls. It seems likely that the breaking up of the soil in this experimental area in November 1935, prior to sterilization, compelled the subterranean forms to seek retreat under the base of the hedge where they stayed till the approach of the warm weather, hence the strip displayed higher population figures. These observations are unfortunately too few for any definite conclusion. The matter becomes more clear when we take the annual population of the controls into consideration. The average figures of the organisms per sample work out as follows:

Control plots close to the hedge:	
B 02 (enclosed)	143·3
A 01 (unenclosed)	138·3
Control plots away from the hedge:	
B 01 (enclosed)	105
A 02 (unenclosed)	135·8

It will be seen that excepting plot B 01 all the rest closely approximated to one another. The case of B 01 appears rather exceptional, and as it was situated away from the hedge, its low population may have been influenced by some entirely different factors, one of which is suggested below. Leaving this plot aside, it will be seen that the hedge exercised no marked influence on the plots situated in its close neighbourhood.

A comparison of the more important components in these four controls shows that the chief difference in plot B 01 was due to the low proportion of Collembola, Myriopoda and Arachnida (Table 3). On account of its extreme end position this portion of the allotment area was reported to have been less cultivated previously than the others. Under the circumstances its soil had become comparatively more compact. This phenomenon was also observed in the earlier part of the experiment when cultivation was undertaken. It is quite possible that the compactness of the soil may have resulted in the low density of its soil organisms which effected its later developments.

Table 3. *Average soil population per sample in control plots*

	Insects				Other invertebrates				
Control plots	Collembola	Immature forms	Other insects	Total	Myriopoda	Arachnida	Other invertebrates	Total	Grand total
A 01 unenclosed	78·1	17·9	3·5	99·5	22·4	11·2	5·2	38·8	138·3
A 02 unenclosed	61·8	20·9	3·5	86·2	25·4	17·8	6·4	49·6	135·8
B 01 enclosed	41·9	33	4·1	79	12·8	9·1	4·1	26	105
B 02 enclosed	70·6	20·1	8·2	98·9	24·4	14·9	5·1	44·4	143·3

9. Composition of the soil fauna

(a) *General comparison*

The allotment area, excepting for the breaking up of its soil in November 1935, followed by sowing of lawn grass and application of superphosphates, did not receive any other treatment and thus remained under more or less constant conditions. Since intensive study of the soil fauna was carried out here, it is thought to represent the activities of the soil organisms more or less accurately.

In England the soil fauna has always been observed to belong to the following orders. INSECTA: Collembola, Thysanura, Orthoptera (Dermaptera), Thysanoptera, Hemiptera, Lepidoptera, Coleoptera, Diptera, Hymenoptera, and Psocoptera. OTHER INVERTEBRATES: Myriopoda, Arachnida, Isopoda, Oligochaeta, Nematoda and Gastropoda.

In addition to these, a specimen of Protura was discovered in August 1936, but unfortunately could not be identified. It has not so far been recorded in any one of the previous soil investigations, although Williams (1913) found many in turf and soil.

Immature forms (eggs, larvae and pupae) of all the insect orders except Collembola, Thysanoptera and Psocoptera, were frequently encountered in the soil samples. Next to the Collembola (44–58·7 %) they formed 14·3–42·2 % of the total soil fauna (Table 4).

Table 4. *Percentage composition of soil fauna*

	Collembola	Immature forms	Other insects	Total insects	Other invertebrates
Allotment area, unenclosed:					
Control	49·2	14·3	2·6	66·1	33·9
Sterilization 1	53	32·8	3·8	89·6	10·4
Sterilization 2	58·7	29·6	5·0	93·3	6·7
Allotment area, enclosed:					
Control	44	21	6·2	71·2	28·8
Sterilization 1	48·9	42·2	4·6	93·7	6·3
Sterilization 2	53·9	39·3	2·0	95·2	4·8

The highest figures of the total soil population determined by various methods and workers on different types of soil are compared in Table 5. All other estimates of the soil population, excepting that of Ford, are much below similar figures obtained during the present investigations. The population on the allotment controls varied between 61·2 to 67·6 million per acre. In one of the sterilized plots a maximum figure of 513·8 million per acre was recorded in December 1936. Ford confined his attention to a richly populated habitat (ridges of a meadow land) and carried out his observations only during those periods of the year when one would have expected the figures to be high. Under such circumstances his estimate was bound to be high, and with the present method it might have been still higher.

(*b*) *Controls*

In the calculation of the monthly means of the fauna both the controls and the two corresponding sterilized plots in the unenclosed and the enclosed areas have been considered together. The mean soil populations of the controls (Table 6) approximated to each other, viz. 67·6 million per acre in the unenclosed and 61·2 million in the enclosed. The difference of 6·4 million per acre in the enclosed control is mainly due to the abnormal behaviour of plot B 01 already discussed. The prominent constituents of the entire association were Collembola, Diptera and Coleoptera, and to some small extent Hemiptera and Hymenoptera (among insects), and Myriopoda, Arachnida and Oligochaeta (among other invertebrates). Their density (Figs. 2*a*, 3*a*) is more or less the same, except that Collembola, Coleoptera and Myriopoda in the unenclosed plots and Diptera and Hymenoptera in the enclosed ones showed slightly higher

Table 5. *Soil populations as determined by various methods*

Worker	Year	Locality	Type of soil examined	No. of samples examined	Average invertebrate population per acre in millions	Percentage of population: Insects	Percentage of population: Other invertebrates	Remarks
McAtee	1907	Washington, U.S.A.	Forest floor	1	1·2	24·1	75·9	—
			Meadow land	1	13·6	80·2	19·8	About 73 % were ants
Cameron	1913–14	Cheshire	Glover's meadow	11	0·8	—	—	Insects only
			Alluvial pasture field	14	1·5	—	—	—
Morris	1916–17	Cheshire	Lane field pasture	29	3·5	—	—	Insects only
Morris	1920–21	Rothamsted, Hertfordshire	Broadbalk (arable), manured dung	23	15·1	57·2	48·8	—
			Broadbalk (arable), unmanured	23	5·0	49·9	50·1	—
Thompson	1920–21	Aberystwyth, Cardiganshire	Pasture land	20	19·5	43·8	56·2	—
Edwards	1925–26	Aberystwyth	Pasture	20	27·2–44·6	48·3–69·2	51·7–32·8	—
Ford	1931–33	Oxford	Meadow (ridges)	16	263·8	92·8	7·2	See Note 1
Baweja (Ladell's apparatus)	1935–37	Rothamsted	Allotment, unenclosed, control	61	67·6	66·1	33·9	—
			Allotment, unenclosed sterilization 1	26	98·4	89·6	10·4	—
			Allotment, unenclosed sterilization 2	20	111·8	93·3	6·7	—
			Allotment, enclosed, control	61	61·2	71·2	28·8	—
			Allotment, enclosed, sterilization 1	26	109·0	93·7	6·3	See Note 2
			Allotment, enclosed, sterilization 2	20	110·2	95·2	4·8	—

Note 1. Observations were carried out in two springs and one winter, excluding the intervening summer and autumn, hence his figures are high.

Note 2. In one of these observations population went up to 513·8 million per acre.

numbers. The immature forms of the insects alone formed a density of 9·7 million per acre in the unenclosed and 13·5 million in the enclosed plots, out of which Diptera and Coleoptera constituted 70 and 22·5 % in the former and 88·1 and 8·7 % in the latter. The proportion of insects to other invertebrates was 2 : 1 in the first instance and 2·4 : 1 in the second.

(c) *Sterilized plots*

The study of the mean soil population of the sterilized plots (Table 7) shows that the principal constituents remained the same as in the controls, but the density of their population was markedly different in various groups. Immature forms of insects made up a concentration of 32–46 million per acre in these plots, in which Diptera and Coleoptera predominated as shown under:

Plot	Treatment	Population: immature forms million per acre	Percentage: immature forms	
			Diptera	Coleoptera
Unenclosed:	Sterilization 1	32·253	94·4	3·3
	Sterilization 2	33·062	94·0	4·1
Enclosed:	Sterilization 1	45·999	95·6	3·2
	Sterilization 2	43·333	95·0	3·9

During the period of 13 months' investigation after sterilization 1 and 10 months after sterilization 2, the soil population had not only regained the original figures, but had increased beyond them. This increase reckoned as a proportion of controls varied as given below. Its rate in the enclosed plots was comparatively quicker and slightly higher.

Unenclosed plots:	
Sterilization 1	1·5 times
Sterilization 2	1·7 times
Enclosed plots	
Sterilization 1	1·8 times
Sterilization 2	1·8 times

The proportion of insects and other invertebrates, which was 2 : 1 in the controls, was very much altered, having reached a maximum of nearly 20 : 1 in one of the sterilized plots. The following comparison illustrates this disturbance in detail:

	Control	Sterilization 1	Sterilization 2
Unenclosed	2 : 1	8·6 : 1	13·9 : 1
Enclosed	2·4 : 1	14·9 : 1	19·8 : 1

A further study of the relative increase of the more abundant orders in the sterilized plots (Table 8, Figs. 2*b*, *c*, 3*b*, *c*) shows that among the insects Collembola and Diptera were the foremost to return. With the exception of these two orders, and in addition Hemiptera, Coleoptera and to a lesser extent

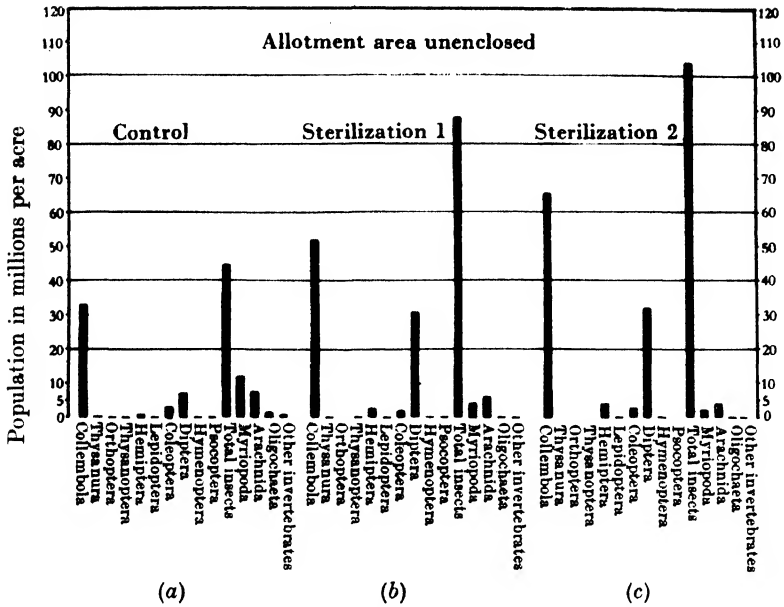


Fig. 2. Mean soil population of the allotment area, unenclosed plots. (a) Control, (b) sterilization 1, (c) sterilization 2.

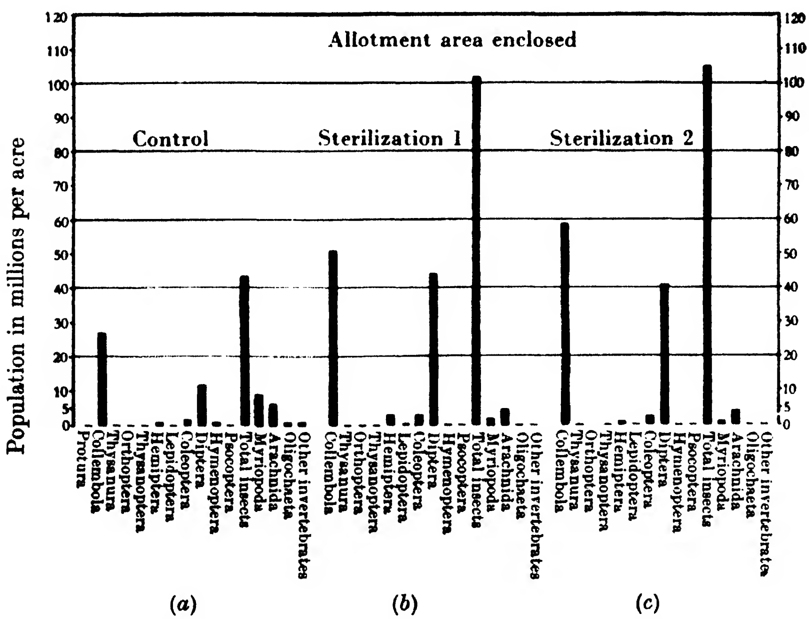


Fig. 3. Mean soil population of the allotment area, enclosed plots. (a) Control, (b) sterilization 1, (c) sterilization 2.

Table 6. *Mean soil population of allotment area controls in millions per acre*

Plot	Insecta: Protura	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Total
Unenclosed	—	33·245	0·209	0·005	0·042	0·889	0·052	3·189	6·848	0·209	0·020	44·708
Enclosed	0·005	26·920	0·157	0·052	0·105	1·202	0·031	1·725	11·918	1·255	0·183	43·553

Plot	Other invertebrates: Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
Unenclosed	12·179	7·527	0·575	1·725	0·627	0·261	22·894	67·602
Enclosed	9·148	6·116	0·157	1·098	0·993	0·078	17·590	61·143

Table 7. *Mean soil population of sterilized plots*

Plots	Insecta: Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Total
Unenclosed											
Sterilization 1	52·115	0·314	—	0·02	2·614	0·157	1·986	30·789	0·084	—	88·079
Sterilization 2	65·68	—	—	—	3·947	0·052	2·587	31·886	0·157	—	104·309
Enclosed											
Sterilization 1	51·174	0·078	0·02	0·37	3·136	0·522	2·979	44·431	0·157	0·02	102·887
Sterilization 2	59·407	0·078	—	0·105	1·28	0·052	2·405	41·452	0·052	0·105	104·936

Plots	Other invertebrates: Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
Unenclosed								
Sterilization 1	3·92	5·854	0·052	0·261	0·105	—	10·192	98·271
Sterilization 2	2·3	4·312	0·34	0·444	0·078	0·026	7·500	111·809
Enclosed								
Sterilization 1	1·829	4·6	0·261	0·105	0·037	0·037	6·869	109·756
Sterilization 2	0·784	4·286	0·13	0·078	—	—	5·278	110·214

Thysanura and Lepidoptera, none of the other invertebrates was able to reach the normal population in this period. Although Hemiptera show a considerable increase over the control and also Coleoptera to some extent, their relative density was low due to the rapid growth of Collembola and Diptera, which really predominated in the whole course of recolonization.

Table 8. *Relative increase of soil population of the sterilized plots over the control*

Plots	Sterilization	Collembola	Hemiptera	Coleoptera	Diptera	Total insects	Myriopoda	Arachnida	Other invertebrates	Total population
Unenclosed	1	1·6	2·9	0·6	4·5	2·0	0·3	0·8	0·4	1·5
	2	2·0	4·4	0·8	4·7	2·3	0·2	0·6	0·3	1·7
Enclosed	1	1·9	2·6	1·7	3·7	2·3	0·2	0·8	0·4	1·8
	2	2·2	1·0	1·4	3·5	2·4	0·1	0·7	0·3	1·8

Considering the immature forms of insects, it is to be seen that their increase over the controls was 3·3 and 3·4 times in the unenclosed, sterilizations 1 and 2, and 3·4 and 3·2 times in the enclosed, sterilizations 1 and 2. In this series 3·1 and 3·2 times in the former and 3·2 and 3·0 times in the latter were constituted by Diptera alone.

It seems clear that the sterilized soil encouraged the increase of soil organisms, particularly insects, some of which, namely Collembola and Diptera, multiplied very rapidly, not only upsetting the normal ratio but taking the population to a very high level of density.

10. NORMAL SEASONAL CHANGES

In a study of this kind where many organisms belonging to different orders with a multitude of individual and collective variations are involved, it is impossible to consider each one of them separately. Only those which were regularly present during the investigation and formed a high proportion of the population have been selected for discussion. Insects formed a major proportion of the soil fauna, this being chiefly composed of Collembola and the immature forms, which were in turn mostly Diptera. Therefore attention is directed to these groups. Mean monthly population figures per sample are worked out in Tables 9–14. Dividing the figures on these tables by 2 will convert them into approximate population of millions per acre (Baweja, 1937).

(a) *Unenclosed controls*

The population curve (Fig. 4*a*) shows that the total population of the unenclosed controls was considerably lower during the winter. With the approach of warm weather it began to rise gradually and continued to do so till the middle of September, after which there was a sudden increase in some of the soil organisms, a peak being reached by about the middle of November.

Table 9. *Mean monthly soil population per sample. Allotment area, unenclosed, controls*

	Insecta												Other invertebrates							
Mean date of monthly sampling period	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
1 Feb.	28·5	0·3	—	0·1	—	—	0·4	—	—	0·3	13·6	43·2	5·3	12·1	0·7	7·7	0·3	0·3	26·4	69·6
29 Feb.	14·5	0·5	—	0·5	—	—	1·5	—	—	—	13	30	16	9	3·5	3	—	0·5	32	62
28 Mar.	27·7	—	—	—	—	—	1·7	—	0·3	—	6	35·7	29·5	10·7	2·5	1·5	0·3	0·5	45	80·7
25 Apr.	13·7	0·8	—	0·2	—	—	3·6	—	—	—	16·2	34·5	26·6	14·5	3·1	1·8	0·8	0·8	47·6	82·1
23 May	20	0·3	—	0·3	—	—	1·4	—	—	—	4·3	26·3	16·7	10·7	1·6	13	2	—	44	70·3
20 June	33·4	0·1	—	—	0·3	—	2·6	—	0·1	—	9·5	46	32·6	9	0·5	0·8	0·9	—	43·8	89·8
18 July	33·1	1·1	—	—	0·1	—	2·4	0·3	2·4	—	14·1	53·5	33·6	11	0·5	1·3	0·5	—	46·9	100·4
15 Aug.	46	0·1	—	—	1·8	—	2·8	—	0·5	—	17·8	69	25·6	11·4	1	3·7	1·4	—	43·1	112·1
12 Sept.	45·4	0·5	—	—	0·5	—	0·6	—	0·3	—	14·5	61·8	20	8·4	0·5	1·7	0·9	0·5	32	93·8
10 Oct.	135·9	0·6	—	—	1·8	—	1·1	—	0·2	—	30·4	170	33·4	11·8	0·8	2·1	2·9	—	51	221
7 Nov.	206·5	0·4	—	—	0·6	—	2·5	0·6	0·4	0·4	27·1	238·5	26·5	24·2	0·6	4·3	1·6	0·4	57·6	296·1
5 Dec.	95·4	0·3	0·2	—	1·1	—	1·1	—	—	—	29·4	127·5	20·4	14·9	—	1·5	2·8	2	41·6	169·1
1937																				
2 Jan.	107	0·2	—	—	0·8	—	2·1	—	0·4	—	34·8	145·3	18·3	24·5	0·5	1·9	0·4	0·5	46·1	191·4
30 Jan.									No observations made											
27 Feb.	83·5	—	—	—	—	—	2·5	—	0·5	—	29	115·5	21·5	29·5	—	2	2	1·5	56·5	172

Table 10. *Mean monthly soil population per sample. Allotment area, unenclosed plots—sterilization* 1

	Insecta												Other invertebrates							
Mean date of monthly sampling period	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
29 Feb.	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	0	0
28 Mar.	2·5	1·5	—	—	—	—	—	—	0·5	—	1·5	6·0	5	1·0	—	—	—	—	6·0	12
25 Apr.	4·5	—	—	—	—	—	1·5	—	—	—	4·5	10·5	1	—	—	—	—	—	1	11·5
23 May	14·5	—	—	—	—	—	—	—	—	—	7	21·5	6·5	1	—	—	—	—	7·5	29
20 June	11	—	—	—	1	—	1·5	0·5	—	—	6	20	7·5	—	—	—	—	—	7·5	27·5
18 July	42·5	—	—	—	0·5	—	3·5	0·5	—	—	28	75	9·5	5·5	0·5	0·5	—	—	16	91
15 Aug.	46·5	—	—	—	1·5	—	0·5	0·5	0·5	—	17·5	67	2	2·5	0·5	—	—	—	5	72
12 Sept.	56·5	—	—	—	2	—	1	—	1	—	19·5	80	8·5	8·5	0·5	2·5	1	—	21	101
10 Oct.	167·5	2	—	—	5·5	—	4	1	—	1	138·5	319·5	21·5	15	—	0·5	0·5	—	37·5	357
7 Nov.	175·5	—	—	—	13	—	2	1	—	—	166·5	358	5·5	27	—	1	0·5	—	34	392
5 Dec.	231·5	0·5	—	—	3·5	—	2	0·5	—	0·5	157·5	396	9·5	27	—	0·5	—	—	37	433
1937																				
2 Jan.	262	1	—	0·5	20·5	—	5	2·5	—	0·5	150	442	11	38·5	—	1·5	—	—	51	493
30 Jan.	No observations made																			
27 Feb.	281·5	—	—	—	7·5	—	2·5	1	—	—	105·5	398	10	19	—	0·5	0·5	—	30	428

Table 11. *Mean monthly soil population per sample. Allotment area, unenclosed plots—sterilization* 2

	Insecta												Other invertebrates							
Mean date of monthly sampling period	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
23 May	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	0	0
20 June	1	—	—	—	—	—	2	—	—	—	3·5	6·5	1·0	2·0	—	—	—	—	3·0	9·5
18 July	5	—	—	—	1·5	—	2·5	—	—	—	13·5	22·5	—	4·0	—	—	—	—	4·0	26·5
15 Aug.	35	—	—	—	8	—	1·5	0·5	—	—	28·5	73·5	3	2	0·5	1·5	—	—	7	80·5
12 Sept.	43·5	—	—	—	7	—	1	0·5	1	—	29·5	82·5	3·5	2	—	1·5	—	—	7	89·5
10 Oct.	59·5	—	—	—	2·5	—	2	—	—	—	99·5	163·5	7·5	3	1·5	0·5	0·5	—	13	176·5
7 Nov.	179	—	—	—	11·5	—	1	5·5	—	—	79·5	276·5	11·5	6·5	0·5	1	—	—	19·5	296
5 Dec.	227	—	—	—	6·5	—	5	5·5	—	—	95·5	339·5	10	23	—	1	—	0·5	34·5	374
1937																				
2 Jan.	298·5	—	—	—	2·5	—	7	1	0·5	—	129·5	439	2·5	25·5	1·0	0·5	—	—	29·5	468·5
30 Jan.	No observations made																			
27 Feb.	408	—	—	—	26·5	—	1·5	2·5	—	—	153·5	592	5	14·5	3	2·5	1	—	26	618

Table 12. *Mean monthly soil population per sample. Allotment area, enclosed controls*

	Insecta													Other invertebrates							
Mean date of monthly sampling period	Protura	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																					
1 Feb.	—	24·3	—	—	0·3	—	—	0·2	—	0·2	0·2	8·0	33·2	2·2	9·3	0·2	2·6	—	0·3	14·6	47·8
29 Feb.	—	15	—	—	—	—	—	1	—	—	—	15	31	4	7	1	1·5	0·5	—	14·0	45
28 Mar.	—	26·2	0·7	—	—	0·7	—	0·3	—	16·3	—	30	74·2	17·2	8·6	—	0·5	1	0·2	27·5	101·7
25 April	—	27·1	0·2	—	—	—	—	1·2	—	0·2	—	20·8	49·5	17·8	31·7	0·3	4	3·3	0·7	57·8	107·3
23 May	—	23·6	0·3	0·7	—	—	—	1·0	—	0·7	—	11·7	38	16·3	5·7	0·3	7·7	3	0·3	33·3	71·3
20 June	—	24	—	—	0·3	0·5	—	0·5	0·4	3·6	0·4	8·1	37·8	23·6	6·1	0·6	3	1·5	—	34·8	72·6
18 July	0·1	31·4	0·1	—	—	4	—	1·9	—	3·3	0·2	13·5	54·5	20·5	7·7	0·4	0·9	1	—	30·5	85
15 Aug.	—	41·9	0·6	—	—	2·1	—	0·9	—	3·1	—	12·9	61·5	15·4	5·2	0·5	1	1·4	—	23·5	85
12 Sept.	—	38·4	0·3	—	0·5	2·1	—	1·6	—	0·6	—	18	61·5	12	8·1	0·3	2·6	4·4	—	27·4	88·9
10 Oct.	—	69·2	—	0·2	0·5	—	—	0·3	0·2	0·8	1	43	115·2	24	8·8	—	—	2·5	—	35·3	150·5
7 Nov.	—	145·6	1·1	—	1·2	2·1	—	2·4	0·3	0·9	2·1	55	210·7	34	37·6	0·3	1·5	4·8	0·1	78·3	289
5 Dec.	—	139	0·8	—	0·4	2·8	—	1·2	—	0·5	0·2	44·1	189	23·6	11·9	0·2	1·9	0·4	—	38	227
1937																					
2 Jan.	—	88·6	0·2	—	0·2	1·4	—	0·5	—	—	0·3	46·8	138	22·4	10·8	—	2·2	2·2	0·5	38·1	176·1
30 Jan.	No observations made																				
27 Feb.	—	26·5	—	—	—	6	—	2	—	4	0·5	34	73	11·5	5·5	—	0·5	0·5	—	18	91

Table 13. *Mean monthly soil population per sample. Allotment area, enclosed plots—sterilization* 1

	Insecta												Other invertebrates							
Mean date of monthly sampling period	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
29 Feb.	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	0	0
28 Mar.	—	—	—	—	—	—	2·5	—	2	—	0·5	5	2	—	—	—	—	—	2·5	7·5
25 Apr.	12·5	—	0·5	—	—	—	1	—	—	—	1·5	15·5	1	2·5	—	—	—	—	3·5	19
23 May	6	—	—	—	—	—	—	—	—	—	3·5	9·5	1	2	—	—	—	—	3	12·5
20 June	12·5	—	—	—	0·5	—	—	—	—	—	5	18	1	0·5	—	—	0·5	—	2	20
18 July	29·5	—	—	—	1·5	—	5·5	—	0·5	—	43	80	1	6	1	—	—	—	8	88
15 Aug.	73·5	0·5	—	—	3·5	—	1	0·5	0·5	—	25	104·5	3	8·5	1	—	—	—	12·5	117
12 Sept.	70	—	—	—	21·5	—	3	—	—	—	28	122·5	2·5	10·5	—	0·5	—	—	13·5	136
10 Oct.	77	0·5	—	—	2	—	—	—	—	—	83·5	163	8·5	10	0·5	—	—	—	19	182
7 Nov.	240	0·5	—	1	1	—	6·5	6	0·5	—	117	372·5	4	23	2	1	—	1	31	403·5
5 Dec.	313·5	0·5	—	—	1	—	8·5	4·5	—	0·5	231	559·5	5·5	22	1	—	0·5	—	29	588·5
1937																				
2 Jan.	301·5	—	—	—	32·5	—	7	—	—	—	347	688	8	17·5	0·5	0·5	—	—	26·5	714·5
30 Jan.	No observations made																			
27 Feb.	136	—	—	—	3·5	—	2·5	0·5	0·5	—	258·5	401·5	8	12·5	0·5	0·5	—	—	21·5	423

Table 14. *Mean monthly soil population per sample. Allotment area, enclosed plots—sterilization* 2

Mean date of monthly sampling period	Insecta												Other invertebrates							
	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
23 May	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	0	0
20 June	0·5	—	—	—	—	—	—	—	—	—	3	3·5	—	—	—	—	—	—	—	3·5
18 July	9	—	—	—	1	—	1	1	—	—	27	39	1·5	0·5	—	—	—	—	2	41
15 Aug.	31·5	—	—	—	3·5	—	1	0·5	—	—	32	68·5	—	3·5	0·5	—	—	—	4·0	72·5
12 Sept.	40	—	—	—	7	—	1	0·5	—	—	15·5	64	2·5	5	0·5	—	—	—	8	72
10 Oct.	61·5	—	—	0·5	2	—	1·5	0·5	—	—	*98	164	—	4·5	—	—	—	—	4·5	168·5
7 Nov.	273·5	—	—	0·5	0·5	—	1	1	—	0·5	124·5	401·5	1	26	1	1	—	—	29	430·5
5 Dec.	175·5	1·5	—	—	1	—	1·5	0·5	—	0·5	120	300·5	5	12·5	—	—	—	—	17·5	318
1937																				
2 Jan.	241	—	—	—	—	—	3·5	0·5	0·5	1	221	467·5	2·5	24·5	—	—	—	—	27	494·5
30 Jan.	No observations made																			
27 Feb.	304	—	—	1	1·5	—	3	1	0·5	—	188	499	2·5	5·5	0·5	0·5	—	—	9	508

* Discovered colony of 454 *Trichocera* (?) larvae, not included in totals.

It was soon after followed by an equally rapid fall which tended to bring the population back to its winter level.

The insect population curve shows that insects formed a high proportion of the total population—62 % at the beginning of the observations in February 1936. By about the end of April their number had gone down, and the percentage was 42. After this they started increasing and during the peak period formed 80 %. This peak occurred about the second week of November, and at the end of the observations the proportion had dropped to 67 % of the total

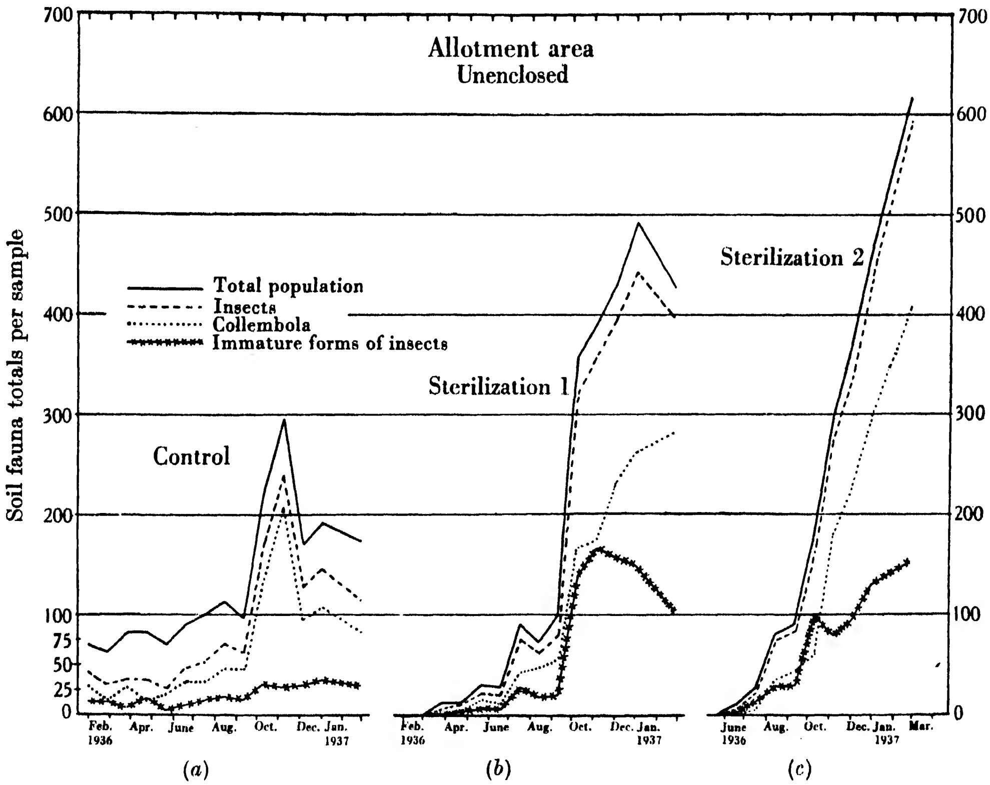


Fig. 4. Monthly variations of the soil fauna (mean numbers per sample). Allotment area, unenclosed plots. (*a*) Control, (*b*) sterilization 1, (*c*) sterilization 2.

population. Collembola formed 41 % at the beginning, and the immature forms (mostly Diptera) 20 %. Collembola then, after a slight rise, fell down to 17 % at the end of April, and growing steadily afterwards formed 70 % of the population during the peak period, falling down to 48 % at the end; while the immature forms fell down to 6 % during the end of May and then gradually increasing came to form 9 % during the peak period and 17 % at the end. The immature forms had in fact increased during summer and autumn, but as their number could not keep pace with the sudden and profuse growth of Collembola their percentage fell.

It will be shown that the weather at the end of April was unfavourable for soil insects in general and Collembola in particular, while the immature forms seemed to suffer a month later, i.e. at the end of May.

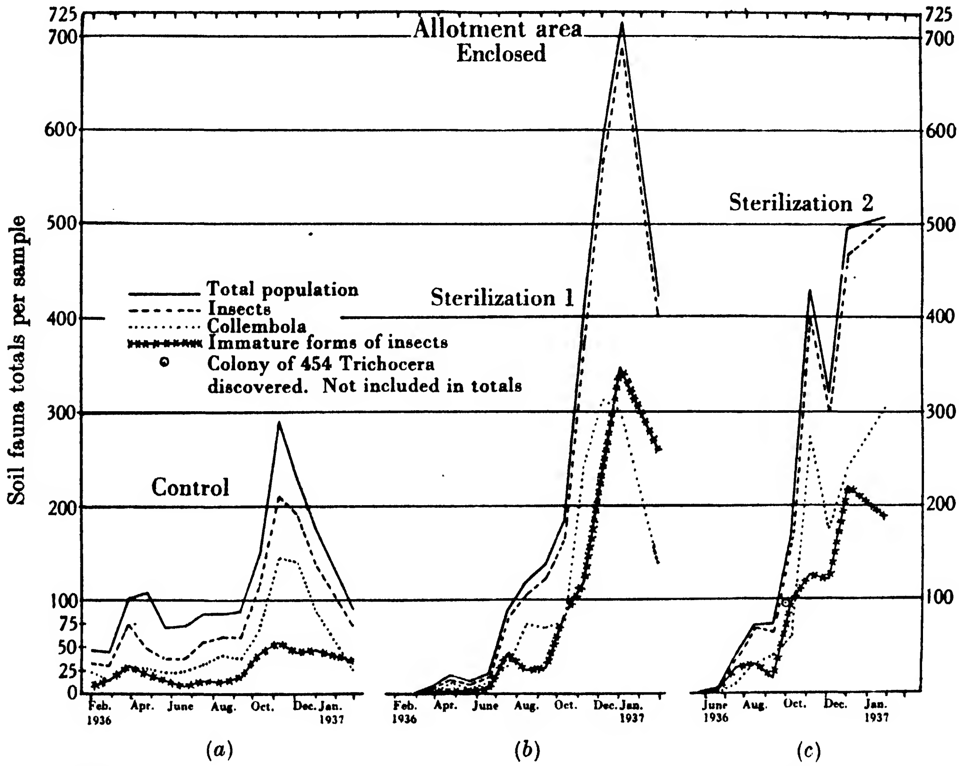


Fig. 5. Monthly variations of the soil fauna (mean numbers per sample). Allotment area, enclosed plots. (*a*) Control, (*b*) sterilization 1, (*c*) sterilization 2.

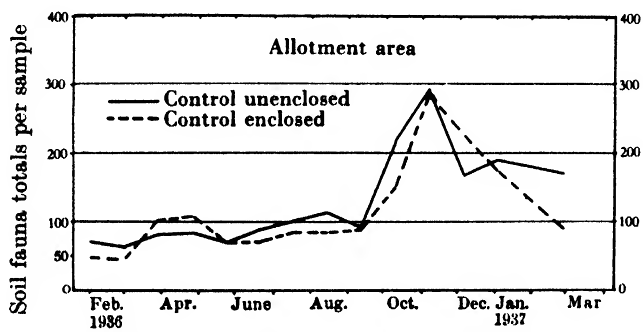


Fig. 6. Comparison of total soil fauna of unenclosed and enclosed controls, allotment area.

(*b*) *Enclosed controls*

The total population of the enclosed controls (Figs. 5*a*, 6) followed more or less the same course as the unenclosed ones except a small rise during March–May. Both (Fig. 6) developed their peaks at the same time, i.e. middle of

November. Insects formed 70% of the total population at the beginning and, as in the case of unenclosed, came down to 46% by the end of April, started rising again and formed 73% during the peak period, and 80% at the end. Collembola started with 51%, fell down to 25% by the end of April, rose to 50% during the peak and ended at 29%. The immature forms started with 17%, and after a slight rise to 19% towards the end of April fell to 15% in the middle of August, increased to 19% during the peak and to 37% at the conclusion of the observations.

It will be seen that the insects in these plots, as well as on the unenclosed ones, showed a decline towards the end of April, Collembola being affected particularly, while the immature forms suffered a little later.

A consideration of these plots shows that the soil population is subject to variations during different periods of the year. The population is at its low level during the winter. With the approach of the warm weather there is a definite tendency to rise and this is maintained throughout the summer. A sudden increase during autumn or early winter, due mostly to the marked increase of Collembola, results in the peak period. The latter is short in duration and is soon followed by an equally rapid fall which tends to bring the population to its original level.

(c) *Effect of atmospheric and soil temperatures on the activity of soil organisms*

The atmospheric temperatures were taken from the meteorological records of the Rothamsted Station, and the soil temperatures were recorded daily at 9 a.m. on the allotment area at a depth of 8 in. Monthly means were worked out in both the cases. The figures, in the case of atmospheric temperatures, were calculated from the mean of weekly maxima and minima. The two temperature curves are shown in Fig. 7. It will be seen that they almost followed the same course. Attention in the following description is, therefore, confined to one of them, viz. the atmospheric temperature.

The allotment area counts were considered to represent accurately the activities of the soil fauna. The unenclosed controls of this area have, therefore, been selected for this study. No organism or group of organisms occurred so regularly as the Collembola. The effect of the above physical factors is probably more pronounced on this order than on any other.

Fig. 7 shows that from the beginning of February to the middle of September, Collembola maintained a low population of 7·2–24·0 million per acre. During this period the mean atmospheric temperature rose from 35 to 61° F. With the gradual fall of the temperature soon afterwards to 45° F. there was a sudden rise in Collembola till the peak was reached in the middle of November. The temperature continued to fall and reached a minimum of 38° F. in early December. A low range of temperature (38–42° F.) then prevailed up to the

beginning of March. The fall of temperature below 45° F. affected the activities of Collembola, and their density fell to 49·9 million per acre in about a month's time. With the prevalence of low temperature, i.e. 38–42° F., their population remained more or less stationary at 43·6–55·9 million per acre.

Several interesting suggestions brought out by this comparison may be summarized as follows:

(1) When the mean atmospheric temperature rises from 38 to 61° F. during spring and summer, Collembola maintain a low population.

(2) When the temperature begins to fall during autumn, the Collembolan activities increase and are at their maximum during a falling range of 55–45° F. which appears to be the zone of optimum temperature.

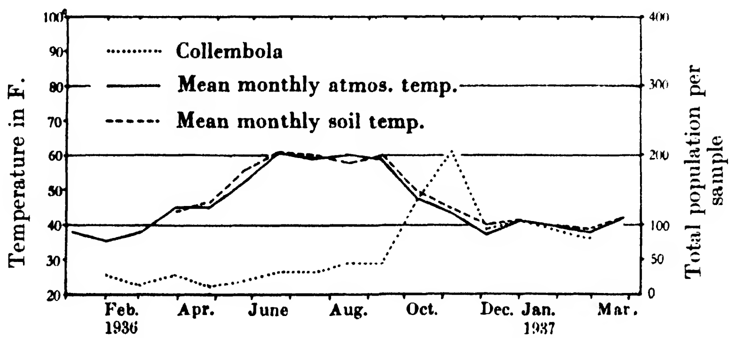


Fig. 7. Effect of atmospheric and soil temperatures on the activity of Collembola.

(3) Temperatures below 45° F. prove inimical to Collembola and their activities are suspended at about 38° F. A further fall below 38° F. is likely to reduce their number.

(4) Since the winter of 1936–7 was comparatively milder than the preceding one, the Collembolan density stood at a higher level. Measuring it in term of highest population figures of the summer months, viz. 24·0 million per acre, it was 1·8–2·3 times more abundant than in the winter of 1935–6.

11. Rate of recolonization of the sterilized plots

(*a*) *Unenclosed plots*

Recolonization in both the instances of sterilization (Table 15, Fig. 8) was much more rapid than was originally expected. The rate of the monthly return of the total soil organisms is worked out below in proportion to the corresponding control. It progressed as follows:

	Size of population in relation to the control in months after sterilization											
	1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	0·15	0·14	0·41	0·31	0·91	0·64	1·08	1·6	1·3	2·6	2·6	2·5
Sterilization 2	0·1	0·26	0·72	0·95	0·8	1·0	2·2	2·4	—	3·6	—	—

The population took 7 months to get beyond the control, and having done so remained far above it, maintaining a density of 2·5 times in sterilization 1 and 3·6 times in sterilization 2 at the end of the observations. The rate in the former was slow for the first four months on account of cold weather, but in the warm weather later on it was very much accelerated. In the second case, since it coincided with the warm conditions, the rate was rapid from the beginning.

Among all other organisms which returned to the sterilized plots (Tables 10 and 11) insects formed, in general, the high proportion of 90–95 %, and were

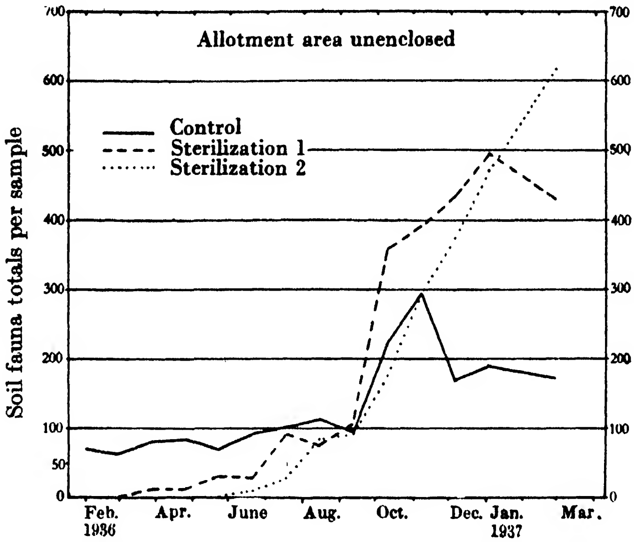


Fig. 8. Rate of recolonization of soil fauna in the unenclosed plots of allotment area.

Table 15. *Recolonization of soil fauna*

Mean date of monthly sampling period	Mean population per sample: Unenclosed plots: Control	Sterilization 1	Sterilization 2	Enclosed plots: Control	Sterilization 1	Sterilization 2
1936						
1 Feb.	69·6	—	—	47·8	—	—
29 Feb.	62	0	—	45	0	—
28 March	80·7	12	—	101·7	7·5	—
25 April	82·1	11·5	—	107·3	19	—
23 May	70·3	29	0	71·3	12·5	0
20 June	89·8	27·5	9·5	72·6	20	3·5
18 July	100·4	91	26·5	85·0	88	41
15 Aug.	112·1	72	80·5	85·0	117	72·5
12 Sept.	93·8	101	89·5	88·9	136	72
10 Oct.	221	357	176·5	150·5	182	168·5*
7 Nov.	296·1	392	296	289	403·5	430·5
5 Dec.	169·1	433	374	227·0	588·5	318
1937						
2 Jan.	191·4	493	468·5	176·1	714·5	494·5
30 Jan.			No observations made			
27 Feb.	172	428	618	91	423	508

* Excluding a colony of *Trichocera* (?) numbering 454.

mainly composed of Collembola and the immature forms. The percentage of their monthly increase relative to the entire population was as follows:

		1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	Insects	50	91	74	73	82	93	79	89	91	91	90	93
	Collembola	21	40	50	40	47	65	56	47	45	53	53	66
	Immature forms	12·5	40	24	22	31	24	19	39	42	36	30	25
Sterilization 2	Insects	68	85	91	92	93	93	91	94	—	96	—	—
	Collembola	10	19	43	49	34	60	61	64	—	66	—	—
	Immature forms	37	51	35	33	56	26	26	28	—	25	—	—

The low percentage of insects in the beginning is due to the large number of other invertebrates; Myriopoda and Arachnida being 41 and 9% in sterilizations 1 and 2, and 21% in sterilization 2 respectively. Among adult insects Thysanura formed 12·5% and Formicidae 4% in the first treatment and Coleoptera 21% in the second. This kept the ratio of Collembola and immature forms low to begin with, but they soon outnumbered the others.

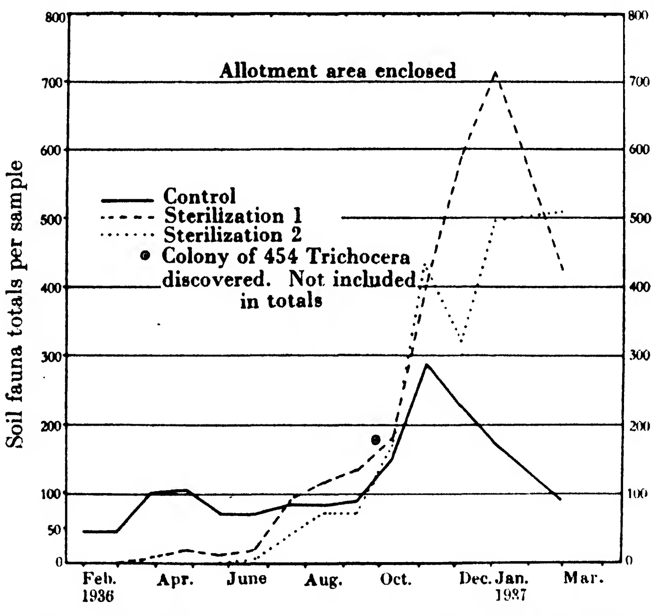


Fig. 9. Rate of recolonization of soil fauna in the enclosed plots of allotment area.

(b) *Enclosed plots*

The rate of recolonization (Table 15, Fig. 9) in the enclosed plots was slightly more rapid than in the unenclosed plots. The population density of the control was passed within five months, after which it continued to grow and at the end of the observations had attained a density of 4·6 times in sterilization 1 and 5·58 times in sterilization 2. The rate of recolonization in proportion to control

is worked out below. As in the unenclosed, it was slower for the first four months in sterilization 1 and quicker in sterilization 2 from the very beginning.

	Size of population in relation to their control in months after sterilization											
	1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	0·07	0·18	0·18	0·28	1·04	1·38	1·5	1·2	1·4	2·6	4·06	4·6
Sterilization 2	0·05	0·48	0·85	0·8	1·12	1·5	1·4	2·8	—	5·58	—	—

Insects (their chief components being Collembola and the immature forms) constituted a major portion of the entire population (Tables 13 and 14). Their percentage of increase in proportion to the total soil population is indicated below.

		Months after sterilization											
		1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	Insects	67	82	76	90	90	89	90	90	92	96	96	95
	Collembola	0	66	48	63	34	63	51	42	59	42	42	32
	Immature forms	7	8	28	25	49	21	21	46	29	49	48	61
Sterilization 2	Insects	100	95	93	90	97	95	94	95	—	98	—	—
	Collembola	14	22	43	56	36	64	55	49	—	60	—	—
	Immature forms	86	66	44	22	58	29	38	45	—	37	—	—

Myriopoda constituted 33%, adult Coleoptera 33%, and adult Formicidae 27% in the beginning of sterilization 1, but did not keep pace with the rapid increase of Collembola. The return, in the case of sterilization 2, was confined to insects alone. The low percentage of immature forms in the first case was due to the passive condition of the insects on account of the prevailing cold.

(c) *Comparison of the total population of simultaneous sterilizations*

(1) *Sterilization* 1 (*in February* 1936) *of unenclosed and enclosed plots.*

The return of the organisms in both cases (Fig. 10) was very slow up to the middle of June, and after this with the increased activity, particularly of insects, on account of warmth, the soil began to exercise its attractive influence. The growth of population in the enclosed plots was greater and the ratio between the unenclosed and the enclosed plots in the peak which occurred in January in both cases stood at 1 : 1·4. By about the following March both had come down to almost the same ratio of 1 : 0·99.

(2) *Sterilization* 2 (*in May* 1936) *of unenclosed and enclosed plots.*

The total population in these instances (Fig. 11) followed a similar course. The recolonization was rapid from the beginning, due to suitable warm conditions. The rise of population continued throughout the period of observation, except one month when there was an abrupt fall in the enclosed plots, but was soon followed again by a sharp jump upwards. Unlike sterilization 1 the population of the enclosed stood slightly below the unenclosed plots with a ratio of 1 : 0·8 at the end of observations.

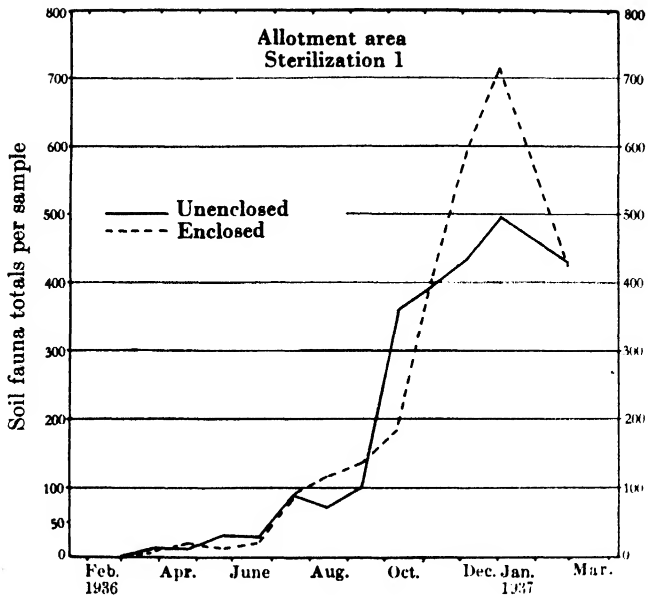


Fig. 10. Comparison of the total soil fauna of sterilization 1 in the unenclosed and enclosed plots of allotment area.

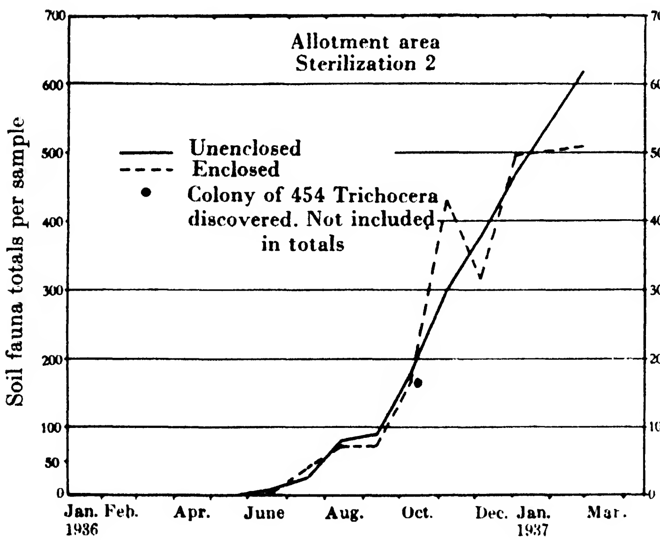


Fig. 11. Comparison of the total soil fauna of sterilization 2 in the unenclosed and enclosed plots of allotment area.

12. Behaviour of some soil population components

Only the predominating or the interesting forms have been selected for this discussion (Table 16). It will be seen that they form 79·6–88·3% of the population. In some cases, for example Collembola, Aphididae, etc., where analysis of individual species was impossible for lack of time, the family has been considered as a whole.

The mean population of each form is in millions per acre, and its percentage is worked out with respect to the total soil fauna (Table 16). The increase is

Table 16. *Behaviour of some soil population components of unenclosed plots in allotment area*

Series no.	Organisms	Control: Mean population in millions per acre	Control: Percentage of total population	Sterilization 1: Mean population in millions per acre	Sterilization 1: Percentage of total population	Sterilization 1: Size of population in relation to control	Sterilization 2: Mean population in millions per acre	Sterilization 2: Percentage of total population	Sterilization 2: Size of population in relation to control
	Collembola								
1	Onychiuridae	14·113	20·9	8·154	8·3	0·6	8·625	7·7	0·6
2	Hypogastruridae	0·836	1·2	15·472	15·7	18·5	18·243	16·3	21·8
3	Entomobryidae	11·029	16·3	17·772	18·1	1·6	24·777	22·2	2·2
4	Isotomidae	7·004	10·4	10·507	10·7	1·5	13·930	12·5	2·0
	Hemiptera								
5	Aphididae	0·073	0·1	0·157	1·8	23·6	3·189	2·9	43·6
	Coleoptera, adults								
6	*Acupalpus meridianus*	0·146	0·2	—	—	—	0·784	0·7	5·4
7	*Amischa analis* Gr.	0·021	0·03	0·366	0·37	17·5	0·261	0·23	12·5
8	*Anommatus 12-striatus* Wesm.	0·46	0·7	0·042	0·04	0·1	0·052	0·05	0·1
	Immature forms								
9	*Harpalus* sp.	0·993	1·5	0·057	0·06	0·06	0·026	0·02	0·03
10	*Homalium* sp.	0·031	0·05	0·209	0·21	6·7	0·392	0·35	12·5
11	*Agriotes* sp.	0·016	0·02	0·042	0·04	2·7	—	—	—
	Diptera, immature forms								
12	*Tipula* sp.	0·026	0·04	0·042	0·04	1·6	—	—	—
13	Chironomidae	1·1	1·6	3·764	3·8	3·4	2·875	2·6	2·6
14	Cecidomyidae	3·554	5·3	18·347	18·7	5·2	14·166	12·7	4·0
15	*Sciara* sp.	0·261	0·4	0·522	0·5	2·0	0·549	0·5	2·1
16	*Scaptomyza disticha* Duda	0·136	0·2	1·725	1·8	12·7	4·783	4·3	35·2
	Hymenoptera								
17	Formicidae	0·157	0·2	0·021	0·02	0·1	0·026	0·02	0·2
	Myriopoda								
18	*Blaniulus guttulatus* Bosc.	6·743	9·9	2·352	2·4	0·3	1·333	1·2	0·2
19	Symphyla	0·042	0·06	—	—	—	—	—	—
	Arachnida								
20	Araneida	0·256	0·4	0·34	0·3	1·3	0·444	0·4	1·7
21	Acarina	6·848	10·1	5·332	5·4	0·8	3·816	3·4	0·6
	Total		79·6		88·28			88·07	

reckoned over the corresponding control. It is obvious from the above comparison that, with a few exceptions, the insects increased rapidly in the sterilized plots and went beyond the control. Only Araneida, among other invertebrates, reached the normal density. Some striking cases are dealt with below.

Collembola. Onychiuridae were regularly present in the control throughout the period of investigation, while Hypogastruridae were only absent towards the end of May. The former composed 20·9 % of the population and the latter 1·2 %. Their behaviour in the sterilized plots was entirely opposite. Onychiuridae failed to regain their normal strength, while Hypogastruridae increased 18·5 and 21·8 times in sterilizations 1 and 2 respectively. Entomobryidae and Isotomidae, which were regularly recovered from the soil, showed an increase of 1·5–2·2 times over the control.

Hemiptera. Aphididae were absent in the control plots up to the middle of July and later they were more or less regularly present; but in the sterilized plots the recolonization was quite marked, starting from the middle of June and continuing till the end of the observations. Their increase amounted to 23·6 times in sterilization 1 and 43·6 times in sterilization 2.

Coleoptera. Beetles occurred as adult as well as immature forms. Nos. 7 and 8 (Table 16) are worthy of some remarks. *Anommatus* 12-*striatus* was present in the controls throughout the period of investigation, with an average population of 0·5 million per acre. It could only regain one-tenth of its normal strength in the sterilized plots. *Amischa analis* on the other hand was recovered once in March in the control and 8 times in sterilization 1 and 4 times in sterilization 2, the relative increase in numbers being 17·5 and 12·5 times respectively.

Harpalus sp. among the immature forms composed a higher population (1·0 million per acre) than *Homalium* sp. (0·03 million) and *Agriotes* sp. (0·02 million); but in the process of recolonization *Homalium* sp. increased 6·7 times in sterilization 1 and 12·5 times in sterilization 2, and *Agriotes* sp. 2·7 times in sterilization 1 and failed to return in sterilization 2; while *Harpalus* sp. only recovered 0·03–0·06 of its original strength.

Diptera. Adults were very uncommon, while immature forms were present in large numbers. Cecidomyidae occurred mostly in over-wintering cocoons. All the Diptera showed a marked increase over the control except *Tipula* sp. which failed to return in sterilization 2. *Scaptomyza disticha* behaved in an interesting manner. It was poorly represented in the controls with an average population of 0·1 million per acre, but its increase in the sterilized plots was very prominent, being 12·7 in sterilization 1 and 35·2 times in sterilization 2.

Hymenoptera. Ants (Formicidae) were encountered in the control in very small numbers, their average population being 0·16 million per acre. During the recolonization process they were discovered once in April in sterilization 1 and once in September in sterilization 2. They thus only succeeded in regaining one-fifth to one-tenth of their normal strength.

Other invertebrates. Among the other invertebrates, Araneida alone succeeded in increasing beyond the control population, while all others failed to regain their normal density. The Myriapod *Blaniulus guttulatus* was a regular soil inhabitant with an average population of 6·7 million per acre in the control. Its rate of recolonization, in the sterilized plots, was strikingly poor. It only managed to recover 0·2–0·3 of its normal strength. Acarina also behaved in the same manner, but their return was a little more rapid. Symphyla occurred occasionally in the controls, but were never found in the sterilized plots.

13. Economic aspect

Sterilization is one of the chief means of pest control inside glasshouses. It increases the soil fertility and, combined with heavy dressings of manure which are not infrequently applied to the plants inside, encourages a luxuriant plant growth. Some of the organisms which gain access to the glasshouses find the new physical conditions favourable and, being protected from their natural enemies, multiply rapidly above and below the surface of the soil, and so assume the status of a pest. The rate of increase of soil animals, particularly insects as already shown, is extremely rapid. Food appears to determine the recolonizing species and sterilization indirectly exerts an influence on their quick return. If, in place of lawn grass, some glasshouse vegetable had been cultivated in the above experiment, the dominating soil organisms would have differed. However, the occurrence of some forms common to the glasshouses and the present experiment is quite interesting.

The springtail *Hypogastrura armata* Nic. is one of the pests of mushrooms inside glasshouses and in the present case Hypogastruridae composed chiefly of *H. armata* Nic. multiplied 18·5–21·8 times over their original strength. A fly, *Sciara* sp., is also another pest of mushrooms. Its increase amounted to double its normal density. Wire-worms, *Agriotes* sp., and leatherjackets, *Tipula* sp., which attack tomatoes in glasshouses, showed an increase of 2·7 and 1·6 times respectively. Aphididae, though not represented by any common species, developed 23·6–43·6 times and it is not surprising to see "root aphis" often occurring on the roots of auriculas and primulas in pots in glasshouses. The Myriapod *Blaniulus guttulatus* did not regain its normal strength, but in presence of strawberry, on which it thrives, its behaviour probably would have been different. These soil organisms might have reacted differently under glasshouse conditions and their number probably would have been much more pronounced. It would be very interesting if such observations could be repeated inside a glasshouse and determinations made as to how soon and in what strength the soil insects or other organisms make their reappearance.

Conditions similar to those in glasshouses are to be met with in tropical countries. The atmospheric temperature during dry summer months is very high and almost sterilizes the soil. Chapman (1931), describing the temperature

of soil communities, remarks: "The annual and diurnal fluctuations of the soil surface on the desert presents probably the greatest temperature fluctuations of any natural environment. Certain Egyptian soils are essentially sterilized each year at the time of the greatest angle of incidence of the sun's rays."

His statement is apparently based on the work done by Taylor & Burns (1924) and Taylor & Williams (1924). While describing the soil temperature observations at Cairo during the "*Sharaqi*" period, Taylor and Burns state: "It may be assumed, therefore, that whenever the minimum screen temperature is 69° F. and at the same time the daily range is 27° F., the soil will become heated to such a temperature that partial sterilization will take place unless some factor other than temperature is introduced to prevent it."

When after such conditions in a tropical country there is a fall of temperature and increase of relative humidity, due to the breaking out of monsoons or excessive irrigation in the following season, conditions very similar to those in glasshouses prevail over a large area. There appears every likelihood of well concealed soil organisms like Collembola and immature forms increasing abnormally and causing damage to field crops. "Root disease" of sugar-cane in Louisiana (Ingram, 1931; Spencer & Stracener, 1930) is attributed in its initial stage to small organisms like *Lepidocyrtus violentus*, *Onychiurus armatus*, etc., followed by the fungus *Pythium*. It is quite possible that the "root rot" of cotton and other field and orchard crops in tropical countries, including India, may be found to originate from the direct damage caused to the tender roots of the young plants by the vast number of these small animals produced during their favourable period of growth. This investigation therefore, in addition, indicates the desirability of research being carried out regarding the recolonization of sterilized soil in the tropics.

14. Comparison of enclosed and unenclosed plots

While it would be unwise to be at all dogmatic about the rate of recolonization in the two sets of plots and the specific nature of fauna recolonizing them, it was, nevertheless, rather surprising that the enclosed and unenclosed plots were recolonized in a similar manner both as regards quality and rate. In fact, the mean population in the enclosed plots was slightly higher in sterilization 1, being 109·0 million per acre against 98·4 million in the unenclosed plots and almost equal in sterilization 2, viz. 110·2 million in the enclosed and 111·8 million in the unenclosed plots.

Three means of recolonization in the sterilized plots were possible: (1) reinfestation from the subsoil, (2) lateral migration, (3) aerial reinfestation.

(1) *Reinfestation from the subsoil.* The soil of Rothamsted, as already pointed out, is sticky clay. A free movement of the soil fauna appears almost impossible. As will be shown under "Subsoil population" (p. 157) ,only a small proportion of the total soil fauna, i.e. 2–14%, exists below 9 in. and possibly

utilize earthworm burrows for their retreat. Besides insects, which formed about half the subsoil population, Myriopoda constituted the major portion of the remaining half. Of the insect population, Collembola (Onychiuridae, Isotomidae and Entomobryidae), formed a concentration up to 4·4 %. The remaining orders were Thysanura, Thysanoptera and Psocoptera. Myriopoda failed to regain their normal strength in the sterilized plots, Onychiuridae also lagged behind, Isotomidae and Entomobryidae attained 1·5–2·2 times their original size. The other minor insect orders were poorly represented in the allotment area and their small numerical strength cannot be expected to effect the soil fauna density in the top 9 in. to any appreciable extent. Under these conditions it is difficult to conceive of any considerable reinfestation from the subsoil. If it existed at all it must have been very slight.

(2) *Lateral migration and* (3) *aerial reinfestation.* Having created empty niches in the soil, one would have expected a more rapid influx of the soil organisms in the unenclosed plots owing to the possibility of lateral migration of the soil organisms in addition to the aerial one. The fact that recolonization averaged 5 months in the enclosed plots and 7 months in the unenclosed ones is opposed to such a notion. Taking the percentage composition of the soil fauna (Table 7) it is seen that the insects formed a comparatively higher percentage in the enclosed controls (viz. 71·2 %) than in the unenclosed (viz. 66·1 %). Immature forms predominated in the former with a composition of 21 % as compared to 14 % in the latter. Similar differences in the number of the immature forms are also noticeable in the sterilized plots of the two sets, i.e. 39–42 % in the enclosed plots and 30–33 % in the unenclosed. These forms could not have increased in the enclosed controls unless reinforced from above and also could not have established themselves and exceeded their original numbers in the sterilized plots without the aerial migration. Had there been any considerable lateral movement of the soil organisms, the immature stages in the unenclosed plots would have far exceeded those of the enclosed. Since this phenomenon did not occur, it appears likely that the lateral migration was quite insignificant. More observations are needed to observe lateral movements of the organisms in the soil, but the aerial migration which is quite evident leads once again to a consideration of another aspect of glasshouse horticulture.

The soil inside glasshouses, like that of the enclosed plots, is surrounded by deep impermeable foundations and the aerial atmosphere is congenial to plant and animal growth. An attraction to sterilized soil has been shown to be pronounced at least with some soil organisms. Hence the dangers of soil contamination are greatly enhanced. Possible sources of soil contamination lie in the use of organic manure, tools and appliances, improper use of screens and ventilators, etc. Once an organism is successful in gaining admission to the inside of the glasshouse, it will soon multiply in strength and, its lateral flow being impossible, inflict heavy losses unless counteracted in time. The use of

sterilized soil, as previously shown, will help to stimulate this already rapid rate of increase. It is, therefore, not surprising to see some of the glasshouse pests exacting a heavy toll on the industry almost every year.

It will thus be evident that the use of sterilized soil, though an effective means of improving soil conditions, has some risks. It is possible that under strict precautionary measures, the contamination of the sterilized soil may entirely or to a great extent be avoided, but if ever it occurs and remains unattended, it may result in serious consequences to the industry.

15. Subsoil population

There has been considerable controversy about the subsoil population in almost all the investigations carried out on the soil fauna. Thompson (1924) remarked: "The soil was examined, occasionally, below the specified depth of the routine samples. Under normal or very moist conditions organisms were of rare occurrence below 9 in.; an occasional *Achorutid* was found. As the soil became dry, *Oligochaetes* began to work their way downwards, and when drought conditions held, a few Symphyla and *Achorutidae* and an occasional insect larva occurred at a depth of from 9 to 12 in., but not lower." She was later on supported by Ford (1935) who observed, "Save for an occasional Lumbricid, no organisms were ever found below a depth of 8 in. and in very few below 4½ in." On the other hand, Morris (1927) stated: "In some groups, no individuals were found at a greater depth than 7 in., although from the diagram it seems probable that the Insects, Collembola and 'Myriapoda' occur to a greater depth than 9 in., at least in plots receiving dung." He was followed by Edwards (1929) who asserted: "The tendency of the modern investigations has been to show that the soil organisms do not descend to greater depths during the winter months. The present data suggest that in lighter type of soils the organisms do descend to deeper levels but in heavier type the reverse is the case."

In the light of such inconsistent views it was deemed desirable to study the soil population as far down as possible. The observations were divided into two sets, the first was carried out in May 1936 and the second in January 1937. Three determinations were made in the former and two in the latter. Since it was difficult to cut a profile 2 or 3 ft. deep, the soil was divided into three layers, viz. top to 9 in., 12–21 in., and 24–33 in. deep, the intervening layers of 3 in. being left, in order to avoid mixing of the soil fauna during sampling. Extra care was taken to plug the sampler with cotton wool to avoid other organisms falling into it from the immediate neighbourhood. Table 17 gives the necessary details and Fig. 12 represents their variation.

A glance at the table shows that the soil population in the top 9 in. varied between 80·4 and 90·7 % and was higher in spring than in winter, while the reverse was the case in the lower two layers, where it increased almost to

twice its spring strength owing to the migration of the fauna downward on account of thermotrōpic responses in winter.

The insect population remained higher in all the three layers in winter than in spring, the comparative increase being marked by a difference of 15·9, 4·7 and 4·4% respectively.

In the case of other soil invertebrates, Myriopoda displayed marked variation. Their concentration was appreciably higher in May, probably due to breeding, and decreased by more than one-third in January in the first layer,

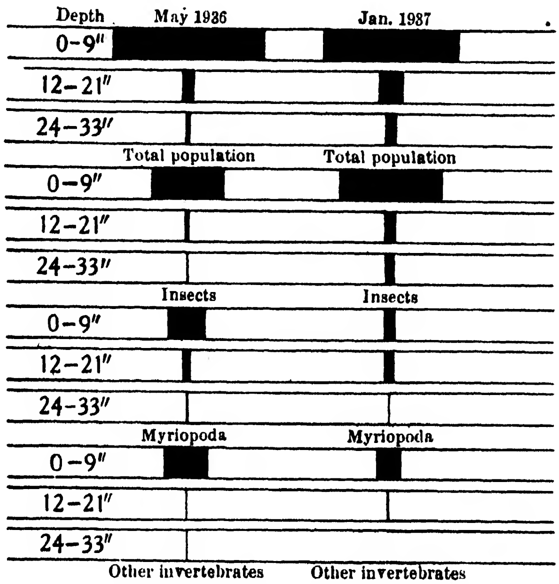


Fig. 12. Depth distribution of soil fauna.

Table 17. *Soil and subsoil population* (%)

Date	Depth (in.)	Insects	Myriopoda	Other invertebrates	Total
May 1936	0– 9	43·4	21·9	25·4	90·7
	12–21	2·2	4·2	0·7	7·1
	24–33	0·95	0·95	0·3	2·2
Jan. 1937	0– 9	59·3	6·9	14·2	80·4
	12–21	6·9	5·6	1·1	13·6
	24–33	5·3	0·7	—	6·0

while it remained almost constant in the bottom two. Besides Myriopoda, all the other invertebrates taken together (in which Arachnida predominated) showed a higher proportion in spring and diminished by about half in winter in the top layer, but maintained a constant ratio in the middle and were absent or practically negligible in the bottom layer in the two seasons.

The subsoil of Rothamsted is sticky clay with a considerable amount of flint. It is hardly likely that any organism can thrive in such anaerobic conditions. Curiously enough, some Lumbricid burrows were traced even below 26 in. and in one instance a worm was dug out at a depth of 24 in. It is, there-

fore, possible for the other soil animals to wander down these mines in pursuit of food.

Two specimens of *Aptinothrips rufus* Gmelin (Thysanoptera) were discovered in each of the second and third layers, and one specimen of *Lepinotus patruelis* Pearm. (Psocoptera) from the second in winter. These delicate insects can hardly be expected to tunnel their way so far down. They must have utilized the earthworm burrows for their retreat.

16. ACKNOWLEDGEMENTS

In addition to the acknowledgement to some of my colleagues at Rothamsted Experimental Station, Harpenden, who are mentioned in the appropriate place in the text, I am deeply indebted to Sir E. John Russell, Director, for providing me with all the facilities during my two years' stay at Rothamsted; to Dr C. B. Williams, Chief Entomologist, for supervision and guidance throughout this investigation; to Major W. R. S. Ladell for the use of his apparatus, and to other members of the Entomological staff, particularly Dr H. F. Barnes, for encouragement and help whenever needed. I am also grateful to the late Dr W. M. Davies, Advisor in Agricultural Zoology, Bangor, for indentification of my collection of Collembola, and for the same purpose to the members of the Entomological and Zoological departments, British Museum (Natural History), particularly Dr K. G. Blair and his assistants for Coleoptera, Dr F. W. Edwards for Diptera, Messrs H. St J. K. Donisthorpe and G. E. Nixon for Hymenoptera, and Messrs F. Laing and W. E. China for Hemiptera. It is also my privilege to be able to express my gratitude to Mr J. V. Pearman, Bristol, for the identification of Psocoptera, Dr Guy Morison, Aberdeen, for Thysanoptera, Dr S. G. Brade-Birks and his assistant Mr S. W. Rolfe, Wye, for Myriopoda and Dr W. S. Bristowe for Araneida.

17. SUMMARY

1. Previous work on the soil fauna is reviewed. It was chiefly confined to the analysis of the density of the soil organisms in relation to their environmental factors.

2. Four plots (9 × 9 ft.) on an allotment at Rothamsted Experimental Station, Harpenden, were sterilized to a depth of 1 ft. in February, and four more in May 1936, by baking the soil to 212° F. Two plots of each set were barricaded by iron sheets 12 in. below and 6 in. above ground and the others left unenclosed. One control was provided for every two treated plots. Lawn grass was later sown on all of them.

3. The effect of sterilization on these plots was studied by taking samples at fortnightly intervals throughout the sequence of 14 months. In all 214 samples were examined from November 1935 to March 1937. Ladell's flotation method was used for isolating the soil organisms. Magnesium sulphate solution with a specific gravity of 1·11 was used as floating medium.

4. Mechanical soil analyses and a survey of the flora are given.

5. The prominent components of the soil fauna were (of insects) Collembola, Diptera, Coleoptera, Hemiptera and to some extent Hymenoptera, and (of other invertebrates) Myriopoda, Arachnida and Oligochaeta. The mean population during the experiment in the control plots varied from 61·2 to 67·6 million and in the sterilized plots from 98·3 to 111·8 million per acre. An analysis of the individual orders and immature forms is included.

6. The soil organisms took seven months in the unenclosed and five months in the enclosed plots to reach a normal density. At the end of observations in March 1937 the number on the sterilized plots had increased from 1·5 to 1·8 times that of controls. The size of different important orders with respect to their control is calculated. With the exception of minor insect orders all other went beyond the normal strength, while none of the other invertebrates save Araneida regained their normal density.

7. The relative proportion of the insects to other invertebrates was considerably affected in the area, viz. from 2 : 1 in the controls to 20 : 1 in one of the sterilized plots. Some of the predominating forms like Onychiuridae, *Anommatus 12-striatus*, *Harpalus* sp., etc. failed to maintain their dominance in the sterilized plots, while some rare ones such as Hypogastruridae, Aphididae, *Amischa analis*, *Agriotes* sp., etc. increased enormously, a striking instance being that of Aphididae which increased 43·6 times over the control.

8. Distinct fluctuations were another feature of the populations. The peak period in the density of their population occurred in late autumn or early winter in the controls and the first set of the sterilized plots. This was caused by the sudden increase of Collembola which was soon followed by an equally sharp decline.

9. The effect of atmospheric and soil temperatures on the variation of Collembola is noted and it is suggested that their numbers increase during a falling range of temperature in autumn (zone of optimum temperature varying between 55 and 45° F.) and that a succession of several mild winters is likely to increase their numbers, with some resulting injurious effect on agricultural crops.

10. The economic aspects of sterilization inside glasshouses and of the baked soils in the tropics are discussed from an entomological point of view. Since both are subjected to heavy infestation of soil organisms, the desirability of further investigation is suggested.

11. A study of the subsoil population showed that a few organisms existed down to a depth of 33 in. Their percentage density varied between 80 and 91 in the top 9 in., being higher in spring than in winter. The reverse phenomenon occurred in deeper layers.

REFERENCES

Adams, C. C. (1915). "An ecological study of prairie and forest invertebrates." Bull. Ill. Lab. Nat. Hist. 11 (Art. 2): 33–280.

Baweja, K. D. (1937). "The calculation of soil population figures." J. Anim. Ecol. 6: 366–7.

Bewley, W. F. (1929). "The practical sterilization by heat of small quantities of soil." J. Minist. Agric. 36: 623–34.

Buckle, P. (1921). "A preliminary survey of the soil fauna of agricultural lands." Ann. Appl. Biol. 8: 135–45.

Cameron, A. E. (1913). "General survey of insect fauna of soil within a limited area near Manchester." J. Econ. Biol. 8: 159–204.

Cameron, A. E. (1917). "The insect association of a local environmental complex in the district of Holmes Chapel, Cheshire." Trans. Roy. Soc. Edinb. 52: 37–78.

Chapman, N. (1931). "Animal ecology with especial reference to insects." New York and London.

Diem, K. (1903). "Untersuchungen über die Bodenfauna in den Alpen." Jb. Naturw. Ges. St Gallen. 1901–2: 234–414.

Edwards, E. E. (1929). "A survey of the insects and other invertebrate fauna of permanent pasture and arable land of certain soil types at Aberystwyth." Ann. Appl. Biol. 16: 299–323.

Ford, J. (1935). "The animal population of a meadow near Oxford." J. Anim. Ecol. 4: 195–207.

Ford, J. (1937). "Fluctuations in natural populations of Collembola." J. Anim. Ecol. 6: 98–111.

Ford, J. (1938). "Fluctuations in natural populations of Collembola and Acarina. Part 2." J. Anim. Ecol. 7: 350–69.

Frenzel, G. (1936). "Untersuchungen über die Tierwelt des Wiesenboden." Jena. 130 pp.

Handschin, E (1929). "Die Tierwelt Deutschlands. Teil 16. Urinsekten oder Apterygota." vi + 150 pp. Jena.

Holdaus, K. (1910). "Die Siebetechnik zum aufsammeln der Terricolfauna (nebst Bemerkungen über die Oekologie der im Erdboden lebenden Tierwelt)." Z. Wiss. InsektBiol. 6, No. 1–4.

Ingram, J. W. (1931). "Soil animals attacking sugar-cane." J. Econ. Ent. 24: 866–9.

Ladell, W. R. S. (1936). "A new apparatus for separating insects and other Arthropods from the soil." Ann. Appl. Biol. 23: 862–79.

McAtee, W. L. (1907). "Census of four square feet." Science, 26: 447–9.

Morris, H. M. (1920). "Observations on the insect fauna of permanent pasture in Cheshire." Ann. Appl. Biol. 7: 141–55.

Morris, H. M. (1922). "The insect and other invertebrate fauna of arable land at Rothamsted." Ann. Appl. Biol. 9: 282–305.

Morris, H. M. (1927). "The insect and other invertebrate fauna of arable land at Rothamsted. Part II." Ann. Appl. Biol. 14: 442–64.

Shelford, V. E. (1913. New ed. **1937).** "Animal communities in temperate America." Chicago.

Spencer, H. & Stracener, C. L. (1930). "Recent experiments with soil animals attacking roots of sugarcane." J. Econ. Ent. 23: 680–84.

Taylor, E. McKenzie & Burns, A. C. (1924). "Soil temperatures during the *Sharâqi* period and their agricultural significance." Bull. Minist. Agric. Egypt, No. 31.

Taylor, E. McKenzie & Williams, C. B. (1924). "A comparison of sand and soil temperatures in Egypt." Bull. Minist. Agric. Egypt, No. 40.

Thompson, M. (1924). "The soil population. An investigation of the biology of the soil in certain districts of Aberystwyth." Ann. Appl. Biol. 11: 349–94.

Vestal, A. G. (1913). "An associational study of Illinois sand prairie." Bull. Ill. Lab. Nat. Hist. 10 (Art. 1): 1–96.

Williams, C. B (1913). "A summary of the present knowledge of the Protura." Entomologist, 46: 225–32.

EXPLANATION OF PLATE 7

The two lower photos show the experimental plots (*a*) at the time of the first soil sterilization, (*b*) at the end of the experiments, with grass which had been sown, and subsequently mown at intervals to permit of soil sampling. The larger plots are 9 ft. square. The smaller ones in (*a*) were used for some preliminary tests. The apparatus to the right in (*b*) is no part of this experiment. Photo (*c*) shows the soil sampling tool.

THE PROTOZOA OF SOME EAST GREENLAND SOILS

By A. DIXON

From the Department of General Microbiology, Rothamsted Experimental Station

1. Introduction

A series of soil samples illustrating stages of plant colonization was collected by Dr and Mrs H. G. Wager on the British East Greenland Expedition (**2**) in the summer of 1936 from Kangerdlugssuak, Lat. 68° 30′ N.

Previous work on the Protozoa of Greenland soils was done by Sandon (**3**) who examined nine samples collected by Dr Morten Porsild at Disko in the neighbourhood of the Danish Arctic Station. His samples were a variety of types, including among them two black peaty soils. On the whole, these samples were rather poor in Protozoa, and in some respects their distribution was unexpected, e.g. one heath soil yielded 15 species of Protozoa—more than soils which were supporting a more luxuriant vegetation.

Sandon's findings show that the climatic conditions do not make the soils of this region unsuitable for the development of Protozoa, since, among these samples, a garden soil enriched every year with poultry manure yielded 46 species, this being the highest number in any of the samples from his world's survey. This garden sample was very rich in Ciliates and Flagellates, but the high numbers were not made up by the testaceous Rhizopoda, as is the case in the soils described here.

The British East Greenland Expedition's samples were taken to a depth of 4 in. and placed in sterile jars which were subsequently sent to Rothamsted for an examination of the protozoan fauna. The observations made were only qualitative, since the time taken in transport precluded any useful quantitative work.

Four media were used for cultivating the Protozoa: peptone agar, soil extract agar, soil extract and hay infusion, and the cultures were kept under observation for four weeks (**1**).

2. Description of samples

The soils are listed according to the stage of plant colonization. With two exceptions, all of them were collected in the region of Kangerdlugssuak, the base of the expedition. The remaining two samples were peaty soils collected

from Angmagssalik about 200 miles farther south. The numbers of species of Protozoa found in each sample are shown in Table 1.

Table 1. *Number of species of Protozoa occurring in each sample*

No. of sample	Rhizopoda: Nuda	Rhizopoda: Testacea	Flagellata	Ciliata	Total Protozoa
6	2	0	3	0	5
4	1	3	5	2	11
9	5	4	8	1	18
1	2	5	9	3	19
8	3	3	8	0	14
2	7	15	9	10	41
5	6	15	6	5	32
7	5	13	7	7	32
3	9	12	10	11	42
10	10	12	13	7	42
1A	4	8	7	3	22
2A	8	16	10	3	37

Sample 6, 10 August. A dry moraine soil near Miki Fjord, *p*H 7·0, stony and grey in colour and showing the first stages of plant colonization. The soil was damp below 1·5 in., though the surface was dry. A few adult plants were scattered about it at wide intervals, also many seedlings which never matured. The following plants were commonly found: *Luzula spicata*, *L. arcuata*, *Trisetum spicatum*, *Oxyria digyna*, *Saxifraga cernua*, and *S. caespitosa*. Only five species.

Sample 4, 11 July. A deposited glacial silt near Miki Fjord, *p*H 6·8, which came from a platform of rock at the base of the moraine mentioned above and forms another early stage in plant colonization. The locality was very wet and the vegetation consisted of *Salix glauca*, *S. herbacea*, *Saxifraga cernua*, *S. oppositifolia* and moss. Eleven species.

Sample 10, 17 August. Soil from just below the largest ruined house of the Skaergaard Peninsula Eskimo settlement, inhabited 150 years ago, *p*H 5·2. This was a dry warm position with a fairly typical vegetation: *Saxifraga cernua*, *Oxyria digyna*, *Draba alpina*, *Erigeron uniflorus*, *Cerastium alpinum*, *Trisetum spicatum*, *Poa glauca*, etc. Forty-one species.

Sample 9, 14 August. Soil consisting of river sand and plant remains, *p*H 5·6, taken from a small, damp plateau, where the soil was frozen from September to the end of May and was boggy in between. The flora on this site included *Salix herbacea* and *Ranunculus glacialis* in great profusion, and *Oxyria digyna*. Eighteen species.

Sample 1, 7 June; *Sample* 8, 11 August. A dark brown soil from red gabbro rock with vegetable remains, *p*H 5·8. In the spring, when sample 1 was taken, the snow had just melted and the soil was wet and the nearby rocks were green with algae. When sample 8 was taken, however, after two months of hot weather, the soil was dry; the flora here was composed mainly of *Salix glauca*, *Erigeron uniflorus*, *Luzula spicata*, mosses and lichens. Nineteen species in sample 1 and thirteen in sample 8.

Sample 2, 12 June; *Sample* 5, 19 July; *Sample* 7, 11 August. A rich vegetation on Thermometer Hill, *p*H 6·2. This position was 180 ft. above sea-level, facing south, and was under a deep snowdrift all the winter. When sample 2 was taken the soil had been exposed for about ten days but was very damp; on the two later dates it had dried. The vegetation was dense, consisting of a mat of *Salix glauca*, *Empetrum nigrum* and *Vaccinium uliginosum* var. *microphyllum*. In sample 2, 40 species and 30 in each of samples 5 and 7.

Sample 3, 10 July. A very rich vegetation site on the lower banks of Miki Fjord, *p*H 5·6. The soil had dried after the melting of the snow and was completely covered with rich vegetation. Among the numerous plant types found were: *Alchemilla alpina*, *A. glomerulans*, *Erigeron uniflorus*, *Cerastium alpinum*, *Veronica fruticans*, *Bartsia alpina*, *Gentiana nivalis* and *Tofieldia palustris*, with patches of *Salix glauca*. There were 43 species.

The soils from Kangerdlugssuak and Miki Fjord showed a transition from moraine to a type of soil composed chiefly of plant remains, which had a peat-like appearance. The only true peats were collected at Angmagssalik on 21 August:

Sample 1 A, *p*H 4·8, from the bank of the main river. The vegetation was plentiful (consisting of *Campanula rotundifolia*, *Luzula spicata*, grasses, sedges and *Chamaenerium* spp., etc.) and was a typical herb field of the district. The Protozoa, 22 species in all, were characteristic of peat.

Sample 2 A, in the same region, from a peat bog of a depth of at least 4–5 ft., *p*H 4·8. The vegetation was characteristic, mainly *Carex rigida*, *Eriophorum Scheuchzeri*, also *Sphagnum* and other mosses. The sample was taken from the top of a peat hag. This site would always be damp, except when it was actually frozen, as the water table was probably 5–6 in. below the level at which the sample was taken. The protozoan fauna was very rich: 39 species.

3. Protozoa present in the soils

The species of Protozoa found in each soil are recorded in Table 2.

All the amoebae found have been previously recorded from soil; it is perhaps worthy of note that *Hartmanella hyalina* and *Naegleria gruberi*, both very common soil forms, were less widely distributed in these samples than previous work would have led one to expect. The dominant species were *Amoeba actinophora*, *Amoeba a*, which was common in seven of the soils, and *Amoeba radiosa*. The last is probably not a true species and is usually regarded as being a stage in the life history of more than one species of amoeba.

The testaceous Rhizopoda were absent from or scanty in the five soils where the vegetation was sparse, but in samples 2, 3, 5 and 7 where the vegetation was rich they were abundant. They also occurred freely in sample 10; this soil, however, is not strictly comparable with the others since there was an increased nitrogen content at this site owing to the previous presence of men and animals.

Table 2.

Soil Protozoa	Samples 1	2	3	4	5	6	7	8	9	10	1A	2A
Rhizopoda nuda												
Amoeba a Sandon	+	+	+	.	+	.	.	.	+	.	+	+
A. verrucosa Ehrbg.	.	.	+	.	+	.	.	.	.	.	.	.
A. diploidea Hartmann & Nägler	.	.	.	.	.	.	+	+	.	+	.	.
A. striata Penard	.	.	+	.	.	+	.	.	.	.	+	+
A. actinophora Auerb.	.	+	+	.	+	+	+	+	+	+	+	+
A. alveolata Mereschk.	.	.	.	.	.	.	.	+	.	+	.	+
A. annulata Penard	.	+	+	.	.	.	.	.	.	+	.	.
A. albida Nägler	.	.	+	.	.	.	.	.	.	.	.	.
A. fluida Gruber	.	+	.	.	.	.	.	.	.	+	.	+
A. radiosa Ehrbg.	.	+	+	.	+	.	+	.	+	+	.	+
A. vespertilio Penard	.	.	.	.	+	.	.	.	.	.	.	.
Naegleria gruberi (Schardinger) Wilson	+	.	.	.	.	.	.	.	.	+	.	+
Hartmanella hyalina (Dang.) Alex.	.	+	.	.	+	.	+	.	.	+	+	.
Biomyxa vagans Leidy	.	+	+	.	.	.	.	.	.	+	.	.
Nuclearia simplex Cienk.	.	.	.	+	.	.	.	.	+	.	.	.
Acanthocystis aculeata Hertw. & Less.	.	.	+	.	.	.	+	.	+	.	.	+
Actinophrys sol Ehrbg.	.	.	.	.	.	.	.	.	.	+	.	.
Rhizopoda testaceous												
Arcella vulgaris Ehrbg.	.	.	.	.	.	.	.	.	.	.	.	+
Pseudochlamys patella Clap. & Lachm.	.	.	.	.	.	.	.	.	.	+	.	.
Difflugia oblonga Ehrbg.	.	.	.	.	+	.	.	.	.	.	.	.
D. globula Ehrbg.	+	+	+	.	+	.	+	.	.	+	+	+
D. constricta (Ehrbg.) Leidy	+	+	+	.	+	.	+	.	+	+	+	+
Cryptodifflugia eboracensis Wailes	.	.	.	.	+	.	+	.	.	.	+	+
Nebela collaris (Ehrbg.) Leidy	.	.	.	.	.	.	.	.	.	.	.	+
N. dentistoma Penard	.	+	.	.	.	.	.	.	.	.	.	.
Hyalosphenia minuta Cash.	.	.	.	.	+	.	.	.	.	.	.	.
Heleopera sp. Leidy	.	.	.	.	.	.	.	.	.	.	.	+
Cochliopodium bilimbosum Auerb.	.	+	+	.	+	.	+	.	.	+	.	+
Euglypha tuberculata Duj.	.	+	+	.	+	.	+	+	.	+	+	+
E. rotunda Wailes	.	+		.	+	.	+	.	.	.	.	.
E. laevis Ehrbg.	.	+	+	.	+	.	+	.	.	+	+	+
Assulina seminulum (Ehrbg.) Leidy	.	+	.	.	+	.	+	.	+	.	.	.
Trinema enchelys (Ehrbg.) Leidy	+	+	+	+	.	.	+	+	.	+	.	+
T. lineare Penard	+	+	+	.	+	.	+	+	+	+	+	+
T. complanatum Penard	.	+	+	.	+	.	+	.	.	+	.	.
Corythion dubium Paranek	+	+	+	.	.	.	.	.	+	+	+	+
C. pulchellum Penard	.	+	+	.	.	.	.	.	.	.	.	+
Sphenoderia lenta Schlumb.	.	+	+	.	+	.	+	.	.	+	.	+
Lecythidium hyalinum Ehrbg.	.	.	+	+	.	.	+	.	.	+	.	.
Pseudodifflugia fulva (Archer) Penard	.	+	.	.	.	.	.	.	.	.	.	.
P. gracile Schlumb.	.	.	.	+	+	.	.	.	.	.	+	+
Microgromia levipes Penard	.	.	.	.	+	.	.	.	.	.	.	+
Mastigophora												
Cercomonas crassicauda Alex.	+	+	+	+	+	+	+	+	+	+	+	+
C. longicauda Stein	+	.	.	+	.	.	+	.	+	.	.	+
Cercobodo agilis Moroff	+	.	+	.	.	.	.	.	+	.	.	.
Helkesimastix faecicola Woodc. & Lap.	.	+	.	.	.	.	.	.	+	.	.	.
Mastigamoeba sp. F. E. Schultze	.	.	.	.	.	.	.	.	.	+	.	.
Monosiga ovata Kent	.	.	.	.	.	.	.	.	.	.	.	+
Phalansterium solitarium Sandon	.	.	.	.	.	.	.	.	.	+	.	.
Bodo celer Klebs.	.	+	.	.	.	+	.	+	.	+	.	.
B. edax Klebs.	+	.	+	.	+	.	+	.	.	.	+	+
B. saltans Ehrbg.	.	.	.	.	.	.	+	.	.	.	+	+
Heteromita globosa Stein	+	+	+	+	+	+	+	+	+	+	+	+
Spiromonas angusta (Duj.)	.	.	+	.	.	.	.	.	.	.	.	.
Sainouron mikroteron Sandon	+	+	+	+	+	+	+	+	+	+	+	+
Allantion tachyploon Sandon	.	+	.	+	.	.	.	+	.	+	+	+
Proleptomonas faecicola Woodcock	.	.	.	.	.	.	.	.	.	+	.	.
Tetramitus spiralis Goodey	+	+	.	.	.	.	.	.	.	+	.	+

Table 2 (*continued*)

Soil Protozoa	Samples 1	2	3	4	5	6	7	8	9	10	1A	2A
	Mastigophora (*cont.*)											
Oikomonas termo Ehrbg.	+	+	+	+	+	+	+	+	+	+	+	+
Scytomonas pusilla Stein	.	.	+	.	.	.	.	.	.	.	.	.
Anisonema minus Sandon	.	.	+	.	.	.	.	.	.	.	.	.
Entosiphon sulcatus (Duj.) Stein	+	+	+	.	+	.	.	+	+	+	.	.
Astasia sp. Duj.	.	.	.	.	.	.	.	.	.	+	.	.
Hexamitus inflatus Duj.	.	.	.	.	.	.	.	.	.	+	.	.
	Ciliata											
Holophrya ovum Ehrbg.	.	.	.	.	.	.	.	.	.	+	.	.
Enchelys farcimen Ehrbg.	.	.	+	.	.	.	+	.	.	.	.	.
Lionotus lamella Ehrbg.	.	+	+	.	.	.	.	.	.	.	.	.
Colpoda cucullus O.F.M.	.	.	.	.	+	.	.	.	.	.	.	.
C. steinii Maupas	.	+	+	+	.	.	+	.	.	.	+	.
Microthorax sulcatus Englm.	.	+	.	.	.	.	.	.	.	.	+	+
Cinetochilum margaritaceum Py.	.	+	.	.	+	.	+	.	.	+	.	+
Pleuronema chrysalis Ehrbg.	+	+	.	.	.	.	.	.	+	.	.	.
Balantiophorus elongatus Schew.	.	.	+	+	+	.	+	.	.	+	.	.
B. minutus Schew.	+	+	+	.	+	.	+	.	.	+	+	.
Blepharisma sp., Py.	.	+	+	.	.	.	.	.	.	.	.	.
Strombidium gyrens Stokes	+	.	.	.	.	.	.	.	.	.	.	.
Uroleptus musculus Ehrbg.	.	.	+	.	.	.	.	.	.	.	.	.
U. mobilis Englm.	.	+	.	.	.	.	+	.	.	+	.	.
Gonostomum affine Stein	.	.	+	.	.	.	.	.	.	.	.	.
Oxytricha pellionella O.F.M.	.	.	.	.	.	.	.	.	.	+	.	.
Pleurotricha lanceolata Ehrbg.	.	+	+	.	+	.	.	.	.	+	.	.
Stichotricha secunda Py.	.	.	.	.	.	.	+	.	.	.	.	+
Vorticella microstoma Ehrbg.	.	+	+	.	.	.	.	.	.	.	.	.
V. striata Duj.	.	.	+	.		.	.	.	.	.	.	.

Of the two peat soils, sample 2A showed a large population of testaceous Rhizopods, while sample 1A yielded lower numbers; these results suggest that the amount of organic matter in the soil, rather than the *p*H value, was the factor controlling the distribution of the Protozoa of this group.

The Flagellates obtained from these soils were species common to most soils, as for example, *Cercomonas crassicauda*, *Heteromita globosa*, *Oikomonas termo*, *Sainouron mikroteron* and *Allantion tachyploon*. These were recorded for almost every sample. *Entosiphon sulcatus*, though only occasionally found in soils, appear to be more common in these Greenland samples, as it was found in seven of them. *Bodo edax* occurred in six samples and *B. celer* in four. The other Flagellates recorded were only found in one or two samples (see Table 2).

In the case of the Ciliates no particular species can be described as typical of these soils. The ones found most commonly were *Balantiophorus minutus*, *B. elongatus*, *Colpoda steinii*, *Cinetochilum margaritaceum*, *Pleurotricha lanceolata* and *Uroleptus mobilis*, which are all usual soil types. *Colpoda cucullus*, one of the commonest of soil Ciliates, was only found in one soil.

4. ACKNOWLEDGEMENTS

My thanks are due to Dr Harold G. Wager of the School of Botany, Trinity College, Dublin, and his wife, who collected these soils and provided the data regarding locality and vegetation.

5. SUMMARY

1. Soil samples from Kangerdlugssuak in East Greenland were examined.

2. The highest number of species of Protozoa occurred in soils producing the richest vegetation.

3. An unusually large number of species of testaceous Rhizopods occurred in non-peaty soils.

4. A large protozoan population was present in soils frozen for nine months of the year.

REFERENCES

1. **Dixon, A. (1937).** "Soil Protozoa; their growth on various media." Ann. Appl. Bio 24: 442–56.
2. **Wager, L. R. (1937).** "The Kangerdlugssuak Region of East Greenland." Geogr. J. 90: 393–425.
3. **Sandon, H. (1927).** "The composition and distribution of the protozoan fauna of the soil." Edinburgh.

ON THE INTRODUCTION AND DISTRIBUTION OF *RANA ESCULENTA* IN EAST KENT

By E. P. SMITH

In the winter of 1934–5 I introduced 12 specimens of the European edible frog, *Rana esculenta* (the Hungarian variety), into a pond beside a running stream in my garden at Stone-in-Oxney, East Kent. The site is an old sea-creek which, in Tudor times, formed a small landing stage; but now, since the sea has receded five miles or more, abuts upon a tract of land where the flats comprising the Walland, Romney and Denge Marshes usurp the place of the salt water. It is a maze of dykes, canals, meres and streams intersecting rich pastures.

I bought the frogs first of all because they are extremely ornamental; their colours vary from a shrill emerald green to a blackish bronze olive. Secondly, I wished to save them from the fate of vivisection; and thirdly, I hoped that they would eat the mosquito larvae with which our still waters abound. These 12 frogs had been kept in cold storage and without food for 18 months before passing into my keeping.

At first nothing happened. When the spring came they sat round the edge of the pond sunning themselves. Then, in May 1935, we discovered their vocal abilities. For weeks on end nobody could sleep on the pond side of the house, and the frogs were becoming a first-class nuisance. Then, in June, two of the largest specimens migrated to a mere about half a mile away; and there set up an unceasing cry to attract their mates to them. This mere had dried up in the drought two years previously, and all the pike in it had died or been caught by hand by the villagers, so, except for an occasional heron, there were no natural enemies. At length, in October 1935, the remaining frogs wandered to the same mere.

My belief is that the first to go went to find a new spawning ground, because they had all mated in the original pond and the fish I keep there (large specimens of roach and golden rudd and golden orfe) had devoured most of the tadpoles. Yet, later in the year 1936, the mere was full of young frogs. During this summer nothing very much happened except that they were all vocal, and the villagers living within half to three-quarters of a mile of the mere began to complain bitterly of the "song". At the same time specimens appeared in Appledore three miles away and connected by a circuitous route of water with the mere.

In May 1937 began what I might call the Great Year of *Rana esculenta*. There was an enormous amount of spawn, and tadpoles and minute frogs were to be seen everywhere. Specimens were located as far away as the Great Lake

at Bedgebury on the uplands 14 miles distant and unconnected by water with the mere. The local suggestion in this case is that the spawn was carried there on heron's legs during the preceding summer, for the frogs seem to be dumb for the first year of their lives. They also appeared at Lydd, nearly 14 miles away (by water) in the opposite direction, but connected by almost continuous dykes with the mere. They were appallingly vocal all through the summer. On warm nights they would give the impression of large armies of ducks contending. Cars would draw up and the occupants get out to enquire what the noise was. The villagers became frantic. They called a parish meeting of protest, and addressed complaints to the Ministry of Health and the M.P. for the Ashford Division of Kent. At this point the Press took a hand. During the "silly season" one newspaper published a long, main-page article, humorous and highly exaggerated, about the singing frogs of Stone-in-Oxney. This resulted in demands for the frogs from all parts. A cunning boy discovered how to catch them and numbers were exported to various places in Scotland, to Sussex and Hertfordshire; while a "line" of about 200 was sold to a firm at Barking Creek to cope with the mosquito plague there. I have not heard whether or not they throve.

But now, in 1938, all has changed. The frogs are still very numerous, far outnumbering the common *Rana temporaria*. But their voices have declined or should I say—abated? Their song is no longer a full-throated, virile epithalamium. It has degenerated into a thin, tinny and intermittent lyric. No longer is there any chorusing. The song is isolated. Here and there a frog will croak; but I am sure no villager has lost five minutes' sleep this year during the breeding season.

This change has been startling and inexplicable. I could have understood a gradual decline; but such a sudden stoppage was quite unlooked for. The frogs are still as numerous as ever; but they are silent. Does it forecast their decline? If the song is an essential to their breeding, it must do. On the other hand, the weather has been hot and very dry, and conditions generally extremely favourable. The small frogs are certainly not as numerous as last year. Or do they breed in cycles? and have we entered upon an unproductive cycle?

Last year they looked like spreading over the whole of south England. To-day it seems as if they would quickly die out.

During the last 3½ years I have made certain observations of their habits, etc., and I append them.

(1) *Rana esculenta* is very migratory. There seem to be two periods of migration—a small one in about June when the older adults leave the younger, and a sort of "general post" in October when they all change their habitat and seek winter quarters. They will take up their abode in a small pond for a year, then completely desert it and return there, after an interval of a year or two, in large numbers. For instance, the ponds in my garden which have been deserted since the autumn of 1935 now contain a dozen or more specimens of

varying size. I imagine this is due to their "combing" a pond of insect life and then forsaking it. During their migratory periods they will cover large tracts of waterless land, as much as two miles. They travel, as far as I can make out, by night; and progress by means of three or four jumps and then a rest, and then on again.

(2) As regards distribution, it is safe to say that during the 3½ years since their importation they have covered a square of some 28 miles; but a great deal of this area is connected together by water. I do not regard their appearance at Bedgebury as an instance of normal progression. They must have been carried there somehow in the form of spawn.

(3) They are very powerful swimmers and very powerful jumpers. One, who was caught and tested, cleared 4 ft. 9 in. The legs of this frog measured just under 11 in.

(4) They do not breed or sing till they are fully 12 months old. After that, they go on growing for at least another two years; but I doubt if they reach their full size till they are four or five years old.

(5) They are shy when approached, but intensely curious; and they can be caught by watching where one has leapt into the water because he is certain, if you wait for a few minutes, to come to the surface and put his head out exactly at the spot where he leapt in.

(6) They have an almost ventriloquial power of "throwing" their voices. This has been noted on numerous occasions. You think there is a "songster" within a few feet of you, but you find, by tracking him down, that he may be 100 or 200 yards away. They love noise. A motor mower at work, or even an aeroplane overhead, and sometimes a human being imitating their croak will set them singing. Nothing, however, stills the frog's song so instantly as the appearance of a heron.

(7) They mate in May and June. The male thrusts the female under water, remaining himself with his head and half his body above the surface. At such times they are easily caught. The nuptial embrace seems to last for about two hours.

(8) The immature specimens have more the appearance of little toads than little frogs. The powerful hindlegs develop much later in *R. esculenta* than in *R. temporaria*.

Apparently, early in the nineteenth century, a Mr Berney brought about 1500 specimens from France and Belgium and turned them loose in the Fens near Stoke Ferry; but they are no longer plentiful. In 1843 the same species was discovered in the Cambridgeshire Fens at Foulmire, 30 or 40 miles from Stoke Ferry, where they were christened "Cambridgeshire Nightingales" or "Whaddon Organs". It would appear from this that they do not survive in large numbers in the British Isles, but only in more or less isolated little groups. And I believe that my thriving colony is on its way to such semi-extinction.

REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 27, No. 1, February 1939)

THE February number of the *Journal of Ecology* consists of 250 pages, including ten papers, various reviews, reports of the 1938 meetings and a list of members of the British Ecological Society.

There are several detailed studies of vegetation, two of which deal with forests: first, a comprehensive analysis of the structure and floristic composition of the Southern Nigerian rain forests by P. W. Richards and, secondly, an account of oakwoods near Killarney by J. S. Turner and A. S. Watt, with reference to the climatic and edaphic peculiarities of the district. Another detailed description of vegetation is that of an area in Spitsbergen (Cape Napier), which was first described sixteen years ago and has now been resurveyed by C. G. Dobbs.

In continuation of his salt-marsh studies (Sections IV and V), V. J. Chapman describes certain soil conditions (chloride content, exchangeable bases and moisture variations), as well as giving details of the salt marsh vegetation, both algal and phanerogamic. Another contribution dealing with coastal biology is a description by T. J. Rees of a community of *Rivularia bullata* growing constantly upon *Balanus balanoides*.

H. Baker and A. R. Clapham contribute detailed observations on the seasonal variation during a period of five years, in the acidity (*p*H) of three representative woodland soils near Oxford. H. H. Mann describes the weed herbage of slightly acid arable soils at Woburn. A somewhat unusual type of study is one by H. Milton on the occurrence of viable seeds buried in natural grassland and salt marsh soils in Wales. C. J. Dawkins describes the factors influencing the formation of tussocks by *Schoenus nigricans* near Oxford and also gives a statistical analysis of the facts of their spatial distribution. B. N. Singh and K. Das also deal with the statistical analysis of vegetation, in this case a further contribution to their analytical studies of the distribution of an Indian weed flora on fallow soils.

The reviews deal with the *Journal of Animal Ecology*; a book on Spanish soils; papers on soil erosion; African vegetation; forest ecology and bibliography; and a regional survey of the Cambridge district.

W. H. PEARSALL.

SOVIET ECOLOGY

D. N. Kashkarov (1938). *Fundamentals of animal ecology.* (In Russian.) 602 pp., 140 text-figs. Moscow and Leningrad. (No price given.)

This is the second, thoroughly revised and expanded, edition of a previous book by the same author published in 1933 under the title "Environment and biocoenosis" (see *J. Anim. Ecol.* (1933) 2: 128). The present edition differs from the first in many respects, since several chapters have been rearranged and at least one entirely new one has been added, dealing with the ecology of domestic animals and acclimatization problems.

The book has gained greatly from the revision as regards the introduction of many new data and theories. On the other hand, some additions are made in such a way that the logical sequence of the whole work is considerably disturbed and unnecessary repetitions result. Another fault of the book, pointed out in the review of the first edition, was the scanty attention paid to literature on insect ecology. This has been somewhat rectified now, but the great store of valuable ecological facts and ideas to be found in the entomological literature (especially Russian) still remains practically untouched. For example, the whole great problem of parasitic insects is dismissed with a casual statement that they are "interesting in practical respect", and their role in the balance of populations and in biological control is not even mentioned.

The author, in his preface to the second edition, states that the first was written under strong influence of American ecologists, but that in the meantime Russian ecology has made great strides. One would, therefore, expect a much greater emancipation from American ideas and methods than is actually the case, since references to American papers still predominate greatly even over the Russian ones, while British and especially Continental work is definitely left in the background. Merely as examples, it may be mentioned that no reference can be found to the extensive Continental work on the ecology and biocoenoses of moors; to the comprehensive books and papers by A. Landsborough Thomson on bird migration (a subject on which a number of partly obsolete books are quoted); and to numerous recent European works on geographical variation in birds and mammals.

The American influence finds a particularly clear expression in that a definitely subordinate place is given to autecology as compared with synecology. The author definitely recommends the beginning of ecological studies from a biocoenosis and gradually descending to the study of ecological relations of its components. This approach may have some theoretical considerations in its favour, but the fact remains that all the most outstanding achievements of modern ecology are based on intensive studies of a single, or a few, animals in relation to their environment, with other members of the biocoenosis being studied as parts of that environment.

The above remarks should not be taken as an adverse criticism of the book as a whole, but serve merely to point out some minor faults in an otherwise excellent and generally up-to-date treatment of animal (especially vertebrate) ecology. B. P. UVAROV.

POPULATION DYNAMICS AND DISTRIBUTION

F. W. Bodenheimer (1938). *Problems of Animal Ecology.* 172 pp., 28 text-figures, numerous tables. Oxford University Press. Price 12*s.* 6*d.*

There are three outstanding features about this book: the patience and industry with which so much evidence from the works of the author and his assistants and from the published papers of other investigators has been amassed and concentrated into so small a space; the success which has rewarded a definite attempt to draw together scattered data into a co-ordinated whole by means of laboratory experiment and observation; and the large proportion of the book which consists of figures.

In his Preface the author expresses the opinion that if any real advance in the understanding of vital problems is to be made, the time has now come for some ecologists at least to return to the laboratory in order to consider what conclusions may be reached from a careful examination of the material obtained in the field, and having formulated their hypotheses, to put them to experimental tests. The justification of this point of view is to be found in the account which follows, in the series of six essays making up the book, of the application of such methods to a variety of problems, which in every case has produced results either conclusive in themselves or providing fresh openings for further work.

The influence on various aspects of animal life of biotic and abiotic factors as well as the physiological reactions of the organism itself, is carefully examined and tested. Besides the more obvious question of distribution, such problems as longevity, population growth and structure, biological equilibrium, sex-determination and geographical variation are considered from the experimental point of view, and in each case some solution is found. The author has also attempted to clear up the existing confusion in the use of such terms as "longevity", "biological control" and "biological equilibrium".

Of particular interest, especially perhaps to those concerned with animals as pests or carriers of disease, is the construction of a series of hyperbolae and life charts which together sum up the life-history of a species, indicating the period of time spent in each developmental stage at any temperature, and the succession of generations, periods of aestivation and hibernation, and the time at which the majority of individuals of each generation have reached a given developmental stage throughout the year. The construction of the hyperbolae is

based on the principle that the life-intensity for each species is a constant depending on time and temperature, and when this constant (determined experimentally) and the variations in temperature for any district are known, the local life-history may be calculated with great accuracy. Furthermore, climographs on which favourable and optimal zones of temperature and humidity are marked can be constructed either to explain observed seasonal numerical fluctuations or to calculate those to be expected in any district in which the species occurs.

It is evident that the author himself is particularly impressed by the influence of climatic conditions, especially that of temperature, on the lives of animals, and he has provided good evidence to support his views. Nevertheless he is willing to allow that no one limiting factor can be ascribed to any species, and indeed the book is noteworthy for the small amount of space devoted to the expression of the author's convictions and the large amount of experimental results provided, from which the reader may draw his own conclusions.

It is unfortunate that a book of such valuable biological content should be marred as this is by a series of easily avoided errors, such as the omission of decimal points and the three arithmetical errors in the table at the bottom of p. 54; the transposition of legends referring to two diagrams in Fig. 13, p. 69; the attributing in a substitution on p. 63 of a positive sign to a negative value; and the expression of values actually to be plotted against each other [$l(x)$] as a product (lx) in Chapter 2. Many of the tables have suffered from excessive condensation and become difficult to follow owing to insufficient explanation or data; the formula for the determination of the intensity of the struggle for existence on p. 72 is at first sight meaningless owing to the omission of a negative sign. An inconsistency causing misunderstanding is the calculation of results correct to one decimal figure from approximations (p. 69). The author recognizes the mathematicophobia of many biologists, and accordingly describes the appearance of the logistic curve followed by the growth of population in *Drosophila* and gives a table of values from which it can be constructed, but there is no illustration of the curve, which would carry more conviction.

In themselves these are all faults which by no means affect the fundamental value of the work, giving rather the impression of hasty correction; but in a book which the author admits and even intends to be difficult, a series of such errors unduly taxes the patience of the reader. There is, however, a more serious fault, where data set out in a table on p. 59 are used in a calculation on p. 58: the calculation is incomprehensible because there is no agreement between the two sets of figures in four cases out of eight, and furthermore, only one of the results shown can be obtained by substituting the figures given in the formula (p. 52) on which this calculation is based.

In fairness to the author it must be stated that this criticism refers chiefly to Chapter 3, and should not be allowed to detract from the value of the book as a whole, which, besides being both illuminating and stimulating, is apparently the only one of its kind available.

ENID NELMES.

BREEDING SEASONS IN MAN AND ANIMALS

(1) **F. H. A. Marshall (1936).** *The Croonian Lecture. Sexual periodicity and the causes which determine it.* Philos. Trans. B, 226: 423–56.

(2) **John R. Baker (1939).** *The relation between latitude and breeding seasons in birds.* Proc. Zool. Soc. Lond., Ser. A, 109.

(3) **Ellsworth Huntington (1938).** *Season of birth: its relation to human abilities.* 473 pp., 104 text-figures, and 2 Appendixes. John Wiley and Sons, Inc., 440 Fourth Avenue, New York, and Chapman and Hall, Ltd., 11 Henrietta St., London, W.C. 2. Price 3.50 dollars.

(1) Dr Marshall has written a very comprehensive review of present knowledge about the reproductive seasons of birds and mammals, dealing more especially with the immediate causes involved. A close correlation between seasonal and sexual cycles is known to exist

in most species, but, although it is generally believed that climatic fluctuations stand in causal relationship to the reproductive activity, the possibility of a pre-established rhythm cannot be ruled out. Considerable attention is paid to the products of the endocrine glands, in particular the pituitary, and to their interrelationships and effects on the gonads. There is a basic internal rhythm of reproduction which depends in the first place on an alternation of periods of rest and activity: the periodic elaboration of gonadal hormones is in correlation with this rhythm.

The most interesting part of this paper deals with the way in which the internal rhythm is regulated according to climatic changes. The author is able to show how environmental factors, of which the most important is light, may completely alter the nature of the internal rhythm, as in the case of Southdown sheep exported from England to South Africa. Immediately after the first lambing in the Southern Hemisphere they change over the time of sexual season and lamb in the southern spring. Light acts as an exteroceptive factor on the nervous system, and thence by way of the anterior pituitary on the gonads. In the case of female mammals the interaction of internal and external factors is not a simple one, for although, in the absence of pregnancy, the ovary alternates regularly between oestrous and luteal phases, when pregnancy occurs the action of the anterior pituitary is changed and it prolongs the luteal period. More normally, however, as in birds and male mammals, the gonads show a rise in activity in correlation with a similar rise in the output of the anterior pituitary.

Marshall pays considerable attention to the part played by the nervous system and the hypophysis in the regulation of the breeding season, and has produced a very thorough review of the main points. He goes on to deal with the phenomena of sexual display and posturing, which he attributes to a selection of those animals which are best able to exercise a mutual stimulation, and thereby secure a more effective synchronization in gonadal activity.

In this paper Marshall has coordinated the literature of a difficult subject in a very clear style, and has also raised a number of points which should provide ample stimulus to both laboratory and field workers. (Further discussion of some aspects of the problem may be found in the review by W. Rowan (1938), Proc. Zool. Soc. London, Ser. A, 108: 51–77).

(2) Dr Baker's paper is an analysis of the breeding season data of a number of birds whose individual ranges cover a wide latitude. There are two main problems. First, the determination, in days per degree of latitude, of how much earlier the breeding seasons occur as one travels away from the Poles; and second, the way in which breeding seasons cross over from one hemisphere to the other. A certain number of species have been carefully selected, and tables have been made to show the times at which they breed in different parts of their range. The breeding season is recorded throughout by the times at which living eggs are found. A long series of diagrams shows exactly the egg-seasons of various groups of birds, and a very ingenious diagram showing the seasonal changes in the position of the sun overhead and in the length of day is so constructed that a tracing of it could be superimposed on the egg-season diagrams. By this means it is at once apparent whether reproduction is occurring during times of lengthening or shortening days, and what is the actual length of the day. Using this method it is found that egg-laying is very rare when the length of day is under 11 hr., but, on the other hand, many birds are laying while the days are shortening, so that neither a long nor an increasing day is necessary for rapid reproduction in birds.

In the latter part of the paper the author enters into a discussion of the immediate factors affecting breeding seasons in tropical and temperate regions. The diagrams show quite clearly that, in the tropics, breeding usually starts before the sun comes overhead. It is unlikely that temperature is an important factor, since, in these regions, the increase is very small. It is more probable that the stimulus from the sun is in the form of its light (both visible and ultra-violet). The rainy season also seems to be of importance as a factor in the breeding of tropical birds. In the case of birds in the temperate zone the main immediate causes are probably temperature and length of day.

One of the most striking and far-reaching results of Baker's analysis is to show that under natural conditions light is only one of the factors concerned in the determination of avian

breeding seasons, and that too much significance may have been attached to the influence of light as a single factor. There is one further point which should be mentioned, namely, the existence of an internal rhythm which certainly affects the time of breeding. The extent to which the factor is effective varies considerably: for instance, some Southern Hemisphere birds living in the Northern Hemisphere may continue to breed at the time of year (on the calendar) when they would normally do so in the Southern Hemisphere, whereas others change over and breed in the northern spring (see Baker & Ranson (1938), Proc. Zool. Soc. Lond., Ser. A, 108: 101–41).

With regard to the breeding of birds whose range crosses the equator, it would be expected from a study of the diagrams (and since the egg-season roughly follows the position of the sun overhead) that there would be two main egg-seasons in the year. This actually happens in quite a number of cases, although most species have a breeding season which is related to the sun either on its southward or on its northward course. There is, however, a great lack of evidence on the breeding seasons of equatorial birds, especially those living just south of the equator.

This very careful analysis by Baker should encourage those who write papers on their observations on tropical birds to make sure that they include careful notes on the breeding seasons, lest their work should have permanent value only as hand-lists for taxidermists.

(3) The papers by Marshall and Baker have shown that our knowledge of the breeding habits and reproductive physiology of a large number of species of birds and mammals is growing, although it is by no means adequate in any one species: the book now under review deals with a subject about which we know even less, and which affects us, as human beings, even more. Prof. Huntington has written an intensely interesting book on breeding seasons in man. The title alone might easily mark his whole work as heterodox, for every zoologist is taught that, with regard to breeding habits, mammals may be divided into three groups: those which only breed at certain times of the year, those whose breeding is susceptible to external influences, and those which breed at any time of the year. It is in the latter group that we are accustomed to class man. Huntington now puts forward the hypothesis that there is an optimum season for human conceptions and births, and that this is influenced by climatic factors. Previously, any slight increase of reproductive activity in man in the spring has only been known from subjective evidence.

This study of the season of birth among large groups of persons in different parts of the world appears to show that seasonal fluctuations in the number of births occur, and that the former are correlated with weather conditions, especially temperature. The analysis of millions of births has been carried out, using records from official documents, from the dates of births in biographical dictionaries, *Who's Who*, genealogical literature and other books of reference, and from the records of schools, hospitals, asylums and prisons (which are listed in an appendix). These data have been worked out in the form of seasonal curves based on the number of births per day in each month, and this is in every case expressed as a percentage of the corresponding average for the year.

The main factors which may influence the seasonal distribution of births are both those which change with the seasons, namely climate, diet, disease and cultural conditions, such as religious fasts or seasonal migrations and vacations; and those which do not change with the seasons, for instance, urbanization, industrialization, non-seasonal migration and the restriction of births. Certain difficulties have been experienced in allowing for the errors introduced by such cultural conditions.

In general there appears to be a basic rhythm, with the maximum of births in early spring in the case of the temperate zones. The data on longevity indicate that a slight change in the season at which children are born makes an appreciable change not only in the length of life, but also in general health and vigour. Further, there is a seasonal variation in the sex ratio at birth, and a correlation between a low sex ratio and favourable climatic conditions. In the first twelve chapters of the book the author is concerned with showing by means of curves based on large numbers of births, that the seasonal distribution of births and its correlation with weather conditions, in particular with the temperature, occurs in most regions of the world.

In the following chapters these conclusions are tested by showing that the effect of environment on physical vigour "ranks with heredity and training as one of the three great factors in determining human capacities". There are, however, difficulties in the way of any clear-cut exposition and these are fully realized by Huntington, who does not try to conceal awkward data. Using the *Dictionary of American Biography*, *Who's Who in America*, and other sources, he gives diagrams showing clearly the season of birth among persons with varying degrees of eminence. Most of these follow the usual curve with a maximum of births in the winter months, January, February and March, and a distinct minimum in the summer, although there are certain exceptional groups in which the degree of eminence seems to vary according to the geographical region.

By classifying the five major occupational groups under the categories of religious leaders, intellectuals, artists, executives and hereditary leaders, and studying the distribution of their births in the four regions, Western Europe, Mediterranean, North America, and Eastern Europe, he finds that the intellectuals, artists, and executives show a marked rise in births round February–March (although the executives' curve is noticeably smoother than the first two), whereas the religious and hereditary leaders, for whom curves are only given for Western Europe, show birth minima in the early spring and maxima in the August–September period! The importance of this particular set of curves seems to lie in the great regularity with which the maxima for births in the intellectual occupations agree with his hypothesis that the weather near the time of conception is closely connected with intellectual capacities.

The examination of the season of birth among persons of eminence has revealed that the annual rhythm in such cases is far more striking than that of the population as a whole. The large amount of material used in reaching this conclusion leaves little doubt as to its validity. This investigation also showed that the season of birth among the criminal and defective classes of any population follows the same type of fluctuation as in the groups showing longevity and eminence. In other words, the more ordinary people in society tend to arise from conceptions showing a fairly well-marked "basic annual rhythm", with its highest point in May for most temperate countries, or in the region of 62° F. for others; whereas in the extreme classes of society the curve of conceptions conforms far more closely to this basic rhythm, and shows a more striking maximum in May.

There therefore exists some correlation between certain temperatures and the number of conceptions, and also a probability that conceptions taking place within this optimum temperature range will give rise to persons differing in abilities or social qualities from the average of the population. In some 80 regions investigated the conceptions tend to reach a maximum at temperatures averaging 62° F. (or 17° C.) for night and day together. The author considers this to be the optimum temperature for conception, and, in support of this, there is further evidence that reproduction increases both when the temperature rises to 62° F. and also when it falls to this level. It may also be significant that Huntington's optimum temperature for conception is about the same as the optimum for physical health in general. Sufficient data are not, at present, available to determine accurately whether light plays an important part in stimulating reproduction in man, and in Huntington's opinion it is of considerably less importance than temperature.

Another problem concerned with the temperature at the time of birth is also discussed. Present-day evidence suggests that the optimum temperature for mental activity is somewhere about 45° F. (or 8° C.). The reason for this is obscure, but it is interesting that the author points out that those children conceived in late spring (at the physical optimum) will be born in late winter at a temperature which, at least in the temperate regions, is in the vicinity of the mental optimum. He suggests that, just as the physical optimum would be an advantage at conception, so also the mental optimum associated with increased mental alertness would originally have been advantageous at the time of birth of unprotected young like those of man.

Although the whole trend of this book is to emphasize the importance of the climatic factors present at conception and birth, this is mainly because this aspect has been neglected by other workers, and the author fully realizes that other factors such as heredity, diet and

mode of life, if taken together, would almost certainly be found to exert a greater effect upon longevity, health, and achievements than the climatic conditions at conception.

The possibilities of a limited season of birth for man are discussed and the initial inconveniences mentioned. The author considers that such an undertaking, resulting in a distinct season of birth in early spring, would, in the long run, be advantageous, although the difficulties of finding an ideal population on which to apply any such regulations are only too apparent.

There are passages in this book where the argument becomes purely teleological, as on p. 8, where we read: "the facts set forth in later pages suggest that man acquired this fundamental rhythm because it favoured the survival of the young". However, this criticism in no way detracts from the value of a book which puts forward so many important points based on an immense body of data. It is, of course, inevitable that many will pick on the arbitrary way in which the author has been forced to judge longevity or achievements, but at the same time these difficulties will make the reader realize the great need for more far-reaching statistical records on human populations.

In the present state of our knowledge on human reproductive activity very little, if anything, is known of the actual physiological effects of the various proximate factors affecting reproduction, and the value of Huntington's book, although extremely difficult to assess at the present moment, seems to lie in two directions. First, he has synthesized his data into an intelligible form, and in so doing has not been afraid to use sources of information which are unorthodox. In the second place, he has shown quite clearly that we must recognize climatic conditions at the time of conception and birth as factors which may be just as important as heredity and training in conditioning the future man or woman.

H. G. VEVERS.

A CALIFORNIAN BIRD POPULATION

Mary M. Erickson (1938). *Territory, annual cycle and numbers in a population of wren-tits* (Chamaea fasciata). University of California Publications in Zoology, vol. 42, no. 5: 247–334, 6 plates, and 16 text-figs. University of California Press, Berkeley, California. Price $1.25.

This is a competent and interesting report of a bird population study by means of coloured rings. The chief interest resides in the fact that the species under consideration, the intermediate wren-tit (*Chamaea f. fasciata*), a sort of ecological analogue of our Dartford warbler, is completely resident, whereas other species worked on by Howard, Nice and others have been mostly migrants.

The habitat and the method of working are first described. Sight identification by means of the coloured bands was employed mostly during the spring and summer, while in the autumn and winter live trap lines were laid, and records obtained from these. The work was begun in 1931 and carried on intensively through 1932 and 1933.

A long discussion on territory describes how an area of 16·7 acres of homogeneous chaparral is occupied by just under 20 pairs of birds, each territory averaging about 0·8 of an acre in extent, variations in size being largely determined by the amount of boundary that has to be defended. Both males and females stay strictly in their territories for practically the whole of the year, some slight relaxation occurring only during the late summer. Thus there is no taking up of winter territories, as in the case of the European redbreast. The young stay in somewhat ill-defined areas about the margin of the breeding grounds until they are either eliminated or absorbed into the breeding stock as vacancies occur.

Another long section deals with the reproductive cycle, though little attention is given to the factors which are responsible for the onset of reproductive behaviour or the way in which the day-to-day routine is modified in the pre-nest-building stage. It is shown that clutches vary in size both with the time of year at which they are laid, and with the age of the female. There appears to be considerable loss both before hatching and before fledging, and more

data upon this aspect would have been welcome; but it appears that the nests were not very easy to find.

In contrast the vital statistics showing the rate of replacement in the population are full and interesting. The average age of birds which have survived their first winter is shown to be 4·43 years, though one male was known which occupied a territory for 10 years. Thus about a fifth of the population was replaced every year and the age distribution showed a large percentage (61) of birds that were 3 years old or over.

The whole paper is a valuable contribution to knowledge of the population dynamics of vertebrates, and illustrates the important uses to which ringing may be put, in addition to the mere indiscriminate marking of migrants which is so popular a recreation in this country.

H. N. SOUTHERN.

FLIGHT

C. Horton-Smith (1938). *The flight of birds.* 182 pp. 17 plates and 30 text-figs. H. F. and G. Witherby, Ltd., 326 High Holborn, London, W.C. 1. Price 7*s.* 6*d.*

This is an avowedly popular account of the main problems involved in bird flight and a certain amount has been sacrificed to easy writing. However, the chapters which are devoted to the mechanical principles concerned and the methods by which birds make the utmost use of their medium are lucid and avoid too great use of technical terms.

A brief summary is first given of the history of investigations into flying principles, and this is followed by a recapitulation of the structural and physiological adaptations to flight found in birds and the origin of the flying habit. There is nothing very new in this; in fact the important work of Steiner on the last problem is neglected.

The third chapter deals with the variations in the structure and function of birds' wings, and discusses the division of them into those of high and low aspect ratio. Some remarks on the relation of these types to habitat are interesting to the ecologist: birds with long, thin wings are chiefly confined to open country, whereas those with blunt wings are found both in closed and open country. The necessity for rapid almost vertical rising in e.g. woods involves a short broad wing, generally slotted, a high energy output, and the ability to rotate the wing laterally. The question of the camber of a wing and the way in which it gives a greater proportion of lift over drag is also discussed here.

Chapter IV on the flight habit endeavours, not very clearly, to divide the types of flight according to the method of feeding, but the next chapter on gliding and soaring contains much of interest, and explains the particular conditions of climate and wind that are essential for this type of flight. Flapping flight is next dealt with in some detail, and figures are given showing that the relative weight of the pectoral muscles to that of the body is greater in birds which flap their wings quickly than in "sailing" fliers; also that in the former the ratio of wing span to body length is less than in the latter.

Final remarks deal with the velocity of flight, giving rough instructions for making estimations; and with safety devices such as the slotted wing-tip which saves the bird from stalling when the angle of incidence becomes high. Some of the plates are not very successful as pictures, but most of them illustrate their points well enough. A glossary and bibliography are appended.

H. N. SOUTHERN.

ISLAND LIFE

R. M. Lockley (1938). *I know an island.* 300 pp., 17 maps and diagrams and 49 photos. George G. Harrap and Co., Ltd., 182 High Holborn, London, W.C. 1. Price 10*s.* 6*d.*

Islands have a double interest to the ecologist because they form comparatively finite units of life and because many of them, especially in the British archipelago, contain peculiar races and species of animals that differ from those of the mainland and often represent

remnants of ancient populations now disappeared elsewhere. In recent years there has been a great growth of interest in these islands, represented by expeditions of individuals and of University groups who have done primary surveys, especially on the islands of the West of Scotland.

We can now say that the faunal peculiarities of small islands round our coast are shown mainly in the small mammal species, and to a lesser extent in the birds, also in the absence from islands of certain common mainland species. But the invertebrate fauna shows comparatively little insular racial development, a situation we may now understand in the light of Hardy and Milne's discovery of the large amount of small animal life that is dispersed by aerial currents. It seems therefore that mass collecting on islands, such as has been practised by recent expeditions, should give place to a deeper study of island population interrelations, for it is here that the island offers its chief scientific interest to the ecologist.

That there is also a strong aesthetic pleasure to be gained from quiet study in these surroundings, with their peculiar combination of sea and land, of completeness and isolation, and of immunity from human disturbance, will already be realized by many. This book successfully communicates that feeling to the reader, and at the same time gives him a very interesting introduction to the conditions on some West European islands, illustrated by first-rate photographs and good maps.

Mr Lockley's primary interest is in birds, and his headquarters on Skokholm in South Wales, where he has organized some important field investigations on bird life. This wider survey includes many out-of-the-way islands, and is illuminated by acute observations on the environment, the life of the inhabitants (where there are any), and the wild animals and plants. We have Skokholm (with its huge colonies of puffins and other sea-birds); Grassholm (famous for its gannetry); Ramsey (a breeding place of seals); Bardsey; the Blaskets (off Kerry); Heligoland (with the German bird migration station); Fair Isle (originally Faeroe—Sheep Island; another breeding place of grey seals); North Ronaldshay (in Orkney); the Faeroes; and the Westmann Islands (off Iceland). Those who read and enjoy (as they certainly will) this book will learn to look on islands and their inhabitants with a new respect and discrimination which will, it is hoped, help to counteract the tendency for visitors to have a solely spoliating mentality.

CHARLES ELTON.

FRESH-WATER ANIMALS

Helen Mellanby (1938). *Animal life in fresh water: a guide to British fresh-water invertebrates.* 296 small pp., 211 text-figures. Methuen and Co., Ltd., 36 Essex St., London, W.C. 2. Price 8*s*. 6*d*.

Here is a serious attempt by a trained zoologist (the author is attached to the Department of Zoology in the University of Sheffield) to provide for schools and for the amateur naturalist a reliable general guide to the invertebrate animals likely to be met with in fresh water. For many years there has been a need for such a book, and many English students have begun by using the American text-book by Ward and Whipple as a substitute.

The treatment is systematic, and the usual method is to describe the characteristics of each family and to give an indication of the further subdivisions within it. There are clear illustrations, mostly original, representing various stages in development, as well as the adults. The degree of detail seems to have been determined by space rather than by logic: there is differentiation between the various species of sponge, hydra, planarian worms and leeches. In other groups the division runs to genera (as with oligochaete worms, Mollusca). The insects are dealt with more briefly still.

The chief criticism one can make of the book is the absence of a good bibliography which would enable the student to follow up any group he is interested in. There are some misprints (as *Gammarus drebeni* for *duebeni*). But on the whole this book can be recommended as a good introduction, and it obviously contains in a highly condensed yet readable form the results of much labour and first-hand knowledge.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts are issued free with the *Journal*. They can also be obtained separately in stiff covers, printed on one side of the page to allow them to be cut out for pasting on index cards, by non-subscribers, from the Cambridge University Press, Bentley House, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, M. Dunbar, C. Elton, F. C. Evans, B. M. Hobby, M. Mare, Barrington Moore, E. Nelmes, F. T. K. Pentelow, H. N. Southern, H. G. Vevers and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. Ecological surveys and habitat notes	
(*a*) Marine and brackish	181
(*b*) Freshwater	182
(*c*) Land	183
(*d*) Small islands	185
2. General reports and taxonomic studies of use to ecologists	186
3. Animal behaviour and the action of environmental factors	188
4. Parasites	193
5. Food and food habits	196
6. Populations	197
7. Migration, dispersal, and introductions	203
8. Reports of organizations	205

1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(a) Marine and brackish

See also **57**, **88**

1. Dep. Sci. Industr. Res. (1938). "Estuary of the river Mersey. The effect of the discharge of crude sewage into the estuary of the river Mersey on the amount and hardness of the deposit in the estuary." 337 pp. (London: H.M. Stationery Office. Price 30*s*.)

A very full account of the physics and chemistry of the formation of mud banks. Few biological data are included, but the occurrence of burrowing forms such as *Macoma balthica*, *Nereis diversicolor*, *Pygospio elegans* and *Corophium volutator* was used as an indication of the age and permanence of the banks.

2. Fischer-Piette, E. (1936). "I. Études sur la biogéographie intercotidale des deux rives de la Manche." J. Linn. Soc. (Zool.), 40: 181–272.

Sessile species were examined at 91 stations along the two coasts. Some species, e.g. *Corallina officinalis*, tend to become abundant at parallel positions on the two coasts. As a whole the species fall into six categories: (1) common at all stations visited, e.g. *Patella vulgata*; (2) types dependent on rock surfaces, e.g. *Patella depressor*; (3) those common at one end of Channel and becoming progressively less abundant, e.g. *Chthamalus stellatus*, common at west end; (4) those abundant in exposed situations, e.g. Algae; (5) those abundant in sheltered situations, e.g. *Mytilus edulis*; (6) capricious species, e.g. *Actinia equina*.

3. Hammond, C. O. (1938). "A broadland calamity." Entomologist, 71: 174–5.

In February 1938, Hickling Broad, Horsey Mere, was completely covered by sea water through a breach in the sea wall. Fresh-water fish perished in thousands and all the birds have left, the bittern being the last to go. The rich dragon-fly fauna has been completely wiped out.

4. Holmes, P. F. & Pryor, M. G. M. (1938). "Barnacles in Horsey Mere." Nature, Lond. 142: 795–6.

Balanus improvisus was found in large numbers on the stems of reeds in Horsey Mere, Norfolk, in July 1938. The water has been very saline since the sea broke through in the spring, to which occurrence the presence of the barnacles is presumably due. The fauna of the area is now a mixture of brackish and fresh-water species. *B. improvisus* is a very euryhaline species, occurring in Holland in water of salinity as low as 1·65 per mille.

5. Howes, N. H. (1938). "A brackish water community near Southend." Essex Nat. 26: 104–7.

An artificial lagoon created by the damming of a creek of the River Roach showed a predominantly sea water fauna. The salinity varied from 21 to 28 per mille and is falling by 1 per mille annually. The present fauna contains 2 genera of Protozoa, 6 of Coelenterata, 1 Nemertine, 4 Annelida, 13 Crustacea, 5 Insecta, 6 Mollusca, 1 Polyzoan and 6 vertebrates. Subsequent selection may give precedence to euryhaline species, e.g. *Palaemonetes varians*, *Platichthys flesus*, while the proportions accidentally shut off may influence the future fauna. (For observations on plants and chemical conditions see also **N. H. Howes** (1937). Proc. Linn. Soc. Lond.: 49–51.)

6. Yonge, C. M. (1937). "The biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.)." J. Mar. Biol. Ass. U.K. 21: 687–703.

An account of the habits, habitat and feeding of these two burrowing Gastropod Molluscs.

7. **Fisher, N. (1937).** "Notes on the British Opisthobranchs. 1. The ecology of *Archidoris flammea* A. & H." J. Conch. 20: 362–8.

8. **Brown, R. S. (1938).** "The anatomy of the Polychaete *Ophelia cluthensis* (McGuire)." Proc. Roy. Soc. Edinb. 58: 135–60.

Contains a preliminary section on habits and distribution.

9. **McMillan, N. F. (1938).** "Marine sponges from N.E. Ireland and Co. Dublin." Irish Nat. J. 7: 44–5.

Records of 15 species include brief field notes on colours of the living animals and in some instances their habitats. A new species of *Axinella* is to be described.

(*b*) Freshwater

See also **3, 4, 46, 52, 58, 59, 88, 125, 183**

10. **Dep. Sci. Industr. Res. (1937).** "Survey of the river Tees. Part 3. The non-tidal reaches—chemical and biological." Tech. Pap. Wat. Pollut. Res., Lond. No. 6: 1–189. (London: H.M. Stationery Office. Price 12*s*. 6*d*.)

An account of a chemical and biological survey of the Tees carried out from 1929 to 1933. Contains extensive floristic and faunistic data, in many cases quantitative. The animals and plants are considered as communities and the effect of sewage pollution on the general ecology of the river is discussed. There is an account of the fisheries, and data on the food of fishes are included. There are also accounts of the chemical and bacteriological processes of the decomposition of sewage and of the chemistry of river water.

11. **Kaufmann, R. R. U. (1938).** "The aquatic Coleoptera of the environs of Pannal Ash, near Harrogate. Part I. Hydradephaga." Ent. Mon. Mag. 74: 245–9.

List, with some ecological details.

12. **Browne, F. Balfour- (1938).** "The aquatic Coleoptera of North and South Lincolnshire." Ent. Mon. Mag. 74: 223–32.

An exhaustive list with interesting ecological details.

13. **Browne, F. Balfour- (1938).** "The aquatic Coleoptera of Ross and Cromarty (East and West Ross), including an *Octhebius* new to Britain." Scot. Nat.: 129–34.

A list of all species so far recorded for the district (50 for East Ross; 17 for West Ross).

14. **Walton, G. A. (1938).** "The British species of *Micronecta* (Corixidae, Hemipt.)." Trans. Soc. Brit. Ent. 5: 259–70.

Includes distributional records and some biological information.

15. **Mosely, M. E. (1938).** "The spinner and its eggs. Observations on the habits of egg-laying spinners and the hatching of their eggs." Salm. Trout Mag. No. 90: 18–23.

Egg-laying habits of Ephemeroptera. Specific identifications are not given.

16. Boycott, A. E. & Oldham, C. (1938). "The Mollusca of the Brecon and Newport and other detached or isolated canals." Proc. Malacol. Soc. Lond. 23: 33–50.

Canal building as an ecological experiment. A study of the Mollusca of the isolated canals of the west country, and a comparison with those of the main canal basin. The presence or absence of the commonest basin species in the isolated canals is taken as a measure of the overland dispersion which they have achieved in the last 100 years.

(*c*) Land

See also **53, 86**

17. Flintoff, R. J., Harrison, D. & Mackley, C. (1938). "Notes on the Hole of Horcum, Saltersgate, North Yorkshire. VI. The Mammalia, Reptilia, and Batrachia." Northw. Nat. 13: 83–92.

The species are listed with notes on abundance, feeding habits and comments of general interest.

18. Gordon, A. (1938). "The bats of Helmsley, North Yorkshire." Northw. Nat. 13: 19–21.

Eight out of the twelve British bats have been found within a few miles radius of Helmsley. Two are especially interesting, *Barbastella barbastellus* which is new to the county and *Rhinolophus hipposideros minutus* which was thought to be extinct in Yorkshire.

19. Whittaker, I. (1938). "Birds of a Lancashire cotton town: being notes on the avifauna of Heywood." Northw. Nat. 13: 136–44.

Supplementary notes to the 1934 publication of this name. The long-eared owl and little grebe have been added to the list of nesting species.

20. Wild, S. V. (1938). "The environments of yellow buntings' singing stations." Northw. Nat. 13: 8–10.

The singing stations of 109 yellow buntings were noted in Cheshire, Staffordshire and the Isle of Man during 1937. The major part of the observation districts is devoted to "mixed" farming. Data show that the birds have a slight preference for root rather than grain crops, but by far the most favoured environments were those least cultivated, i.e. pasture and "waste" land.

21. Stelfox, A. W. (1938). "The birds of Lagore about one thousand years ago." Irish Nat. J. 7: 37–43.

More than 1000 bird bones were recovered from a kitchen-midden in swamp land of Co. Meath. About 30 species were certainly or tentatively identified; these were largely water-frequenting birds and scavengers, but also included a primitive breed of domestic fowl and a number of species now rare in Ireland. Vertebrae were almost completely absent from the collection. A plea is made to archaeologists to preserve all small bones recovered.

22. Jary, S. G. & Stapley, J. H. (1937). "Investigations on the insect and allied pests of cultivated mushrooms. IX. *Tyroglyphus dimidiatus* Herm. (*longior*) Gerv." J. S.-E. Agric. Coll. Wye, 40: 119–29.

Includes the method for the preparation of specimens by means of KOH and Berlese mounting media.

23. **Austin, M. D. & Pitcher, R. S. (1937).** "Investigations on the insect and allied pests of cultivated mushrooms. X. *Sciara variens* Johns., its occurrence within a mushroom house, with a description of the male genitalia." J. S.-E. Agric. Coll. Wye, 40: 98.

24. **Austin, M. D. (1937).** "Investigations on the insect and allied pests of cultivated mushrooms. XI. The long-legged mushroom mite (*Linopodes antennaepes* Banks)." J. S.-E. Agric. Coll. Wye, 40: 115–18.

25. **Jary, S. G. (1938).** "Investigations on the insect and allied pests of cultivated mushrooms. XII. Two more Tyroglyphid mites." J. S.-E. Agric. Coll. Wye, 42: 66–81.

26. **Massee, A. M. (1938).** "Notes on some interesting insects observed on fruit trees in 1937." Rep. E. Malling Res. Sta. 1937: 203–8.

Many unusual host plant records including the following: the Lamellicorn, *Sinodendron cylindricum*, on healthy cherry trees; the flea beetle, *Derocrepis rufipes*, on apple foliage; the shot-hole borer, *Anisandrus dispar*, on Himalaya blackberry; the weevil, *Epipolaeus caliginosus*, on hop roots; the Clavicorn, *Librodor hortensis*, on mummified apples; the puss moth on apple. Also evidence of a partial second brood of codling moth.

27. **Massee, A. M. (1938).** "Coleoptera associated with cultivated fruits." Trans. Soc. Brit. Ent. 5: 223–34.

About 70 species occur on the various sorts of fruits grown in this country, of which a few are found exclusively on apple, pear, plum, etc., but the majority have other host plants besides cultivated fruits. The number of species recorded on fruit has not varied to any extent during the past 40 years, but a few species are more plentiful now than formerly.

28. **Donisthorpe, H. (1938).** "Coleoptera taken at Muckross, near Killarney, in May." Ent. Rec. 50: 92–4.

Includes some ecological notes.

29. **Donisthorpe, H. (1938).** "A preliminary list of the Coleoptera of Windsor Forest." Ent. Mon. Mag. 74: 259–70.

The concluding part of this serial publication. The complete list now includes 1870 species. Some of these, such as *Bembidium 4-pustulatum* and *Aulonium trisulcum*, etc., have increased enormously in numbers in the last few years; others have become very rare and have not been met with for a long time in the forest.

30. **Wright, A. E. (1938).** "Natural habits of *Hydriomena* (*Perizoma*) *taeniata* Steph. (Lep., Geometridae)." Entomologist, 71: 198–200.

A local moth occurring sparingly about the head of Morecambe Bay in both Lancashire and Westmorland, and inland as far as Witherslack and Windermere.

31. **Cooper, B. A. (1938).** "Further notes on *Tyria jacobaeae*." Entomologist, 71: 263–4.

Discusses emergence date and food plant selection of cinnabar moth.

32. Freeman, P. (1938). "Notes on Orthoptera observed in 1937." Ent. Rec. 50: 4–5.

Collecting notes on grasshoppers with some ecological details.

33. Freeman, P. (1938). "The distribution of *Metrioptera roeselii*, Hagenb. in Essex in 1937." Ent. Rec. 50: 7–8.

An account of an attempt to map the range of this very local grasshopper.

34. Wilson, G. Fox (1938). "The glasshouse leaf-hopper, *Erythroneura pallidifrons* Edw." J. R. Hort. Soc. 63: 481–4.

An account of the insect, its food plants and life history, together with an outline of control methods for infestations under glasshouse conditions.

35. Davies, W. Maldwyn (1938). "The aphis *Myzus persicae* Sulz in selected districts of Scotland." Scot. J. Agric. 21: 249–58.

It was recorded from sea-level up to the highest centre visited (850 ft.) and was common both in the north and south. The highest populations occur most frequently at low altitudes and in sheltered gardens in urban areas. High aphis counts on forms in exposed situations or remote from villages were apparently due to the proximity of swedes and other cruciferous crops. The migration of winged aphids to potatoes in June is, in general, determined by the occurrence of days when the maximum temperature exceeds 65° F., the relative humidity is less than 75% and the wind velocity less than 5 m.p.h. The general trend of aphis migration in eastern Scotland is from the west towards the east, since the gentle breezes at the time of these requisite conditions come from the west. In north Wales similar suitable breezes were found to come from the east.

36. Massee, A. M., Greenslade, R. M. & Duarte, A. J. (1938). "Notes on the strawberry aphid (*Capitophorus fragariae* Theob.)." Rep. E. Malling Res. Sta. 1937: 209–12.

Life cycle and ecological notes. It can live all the year round on strawberry and under certain conditions on silverweed.

37. Anon. (1937). "The chrysanthemum midge." J. Minist. Agric. 43: 1158–61.

The suggestion is made that the midge attacking greenhouse *Chrysanthemum* is distinct from the species attacking wild *Chrysanthemum* species, including the ox-eye daisy.

38. Beresford, D. R. Pack- (1938). "Some new and rare Irish spiders." Irish Nat. J. 7: 51–3.

The occurrence of four species new to Ireland and additional records of six other rare species supplements a previous list by the same author.

(*d*) Small islands

See also **80, 178**

39. Atkinson, R. (1938). "Natural history notes from certain Scottish islands —North Rona, the Flannan Isles, Handa Island." Scot. Nat.: 145–7.

Notes on the numbers of birds seen during the summers of 1935 and 1937. There is great wanton destruction annually of bird life and seals, black-backed gulls being untouched. The remains of ten species of birds were found in the carcasses and droppings of these gulls.

40. Stewart, M. (1938). "Natural history notes on certain Scottish islands. Sule Stack, Sule Skerry, North Rona, Sula Sgeir and St. Kilda." Scot. Nat.: 107–14.

Notes on the variations in numbers of birds (especially gannets, puffins, kittiwakes, and fulmars) with suggestions for the causes. There are a few topographical and habitat notes. Grey seals, rabbits, earwigs and wood-lice are also noted on Sule Skerry, and mice on St Kilda. There are two maps.

41. Elton, C. (1938). "Notes on the ecological and natural history of Pabbay, and other islands in the Sound of Harris, Outer Hebrides." J. Ecol. 26: 275–97.

These notes describe the vegetation, with evidence of former woodland, the natural conditions, past and present, and history of human occupancy in relation to the present animal life on the islands and in adjacent waters. Pabbay had a large human population until about 100 years ago.

42. Campbell, J. L. (1938). "The Macrolepidoptera of the Parish of Barra." Scot. Nat.: 153–63.

A list of 131 species (69 Noctuidae) recorded between 1935 and 1937 in the Civil Parish of Barra which includes some small islands. The Noctuids were collected chiefly by sugaring, and at sallow, stock, elder and ragwort. Car head-lamps were also used, but a light trap met with little success.

43. Harrison, J. W. Heslop (1938). "A further occurrence of *Zygaena achilleae* Esp. in the Inner Hebrides." Entomologist, 71: 175.

Cocoons of Zygaenid moths from Eigg and Muck yielded *Z. filipendulae* while three *Z. filipendulae* and one *Z. achilleae* were bred from the Eilean nan Each group. *Z. filipendulae* is also recorded from Skye.

44. Harrison, J. W. Heslop (1938). "*Argynnis selene*, a butterfly new to the Isle of Rhum." Entomologist, 71: 213.

Previously recorded from Soay and Skye.

45. Harrison, J. W. Heslop (1938). "The Rhopalocera of the islands of Rhum, Eigg, Muck, Eilean nan Each and Heisker (Inner Hebrides), and of Harris, North Uist, South Uist, Eriskay, Taransay and the Monach Islands (Outer Hebrides)." Entomologist, 71: 265–7.

Fourteen species of butterflies occur in these islands.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

See also Section 4

46. Jenkin, B. M. & Mortimer, C. H. (1938). "Sampling lake deposits." Nature, Lond. 142: 834–5.

Describes a new form of apparatus for taking samples of deposits from the bed of lakes etc. By means of rotating half-cylinders a core can be obtained from any depth, undistorted by compression, a disadvantage formerly associated with all forms of mud samplers.

47. Deraniyagala, P. E. P. (1938). "The loggerhead turtles in the National Museum of Ireland, with special reference to those taken in Irish waters." Irish Nat. J. 7: 66–70.

Systematic and distributional notes on the museum collection of Carettidae, including the recognition of Irish specimens of *Colpochelys kempi*, which is normally restricted to waters of the Gulf of Mexico.

48. Burr, M. (1938). "The Orthoptera of North Germany." Ent. Rec. 50: 146–8.

Comparison with the British fauna.

49. China, W. E. (1938). "Corrections and additions to James Edwards' catalogue of British Hemiptera-Homoptera, Perth, 1908 (excluding Psyllidae)." Ent. Mon. Mag. 74: 191–7.

An important revision of the list of British species and of their nomenclature.

50. Thomas, D. C. (1938). "An annotated list of species of Hemiptera-Heteroptera not hitherto recorded for Middlesex." Entomologist, 71: 148–53.

Records 88 new species, bringing the county total to 242, with notes on abundance, etc.

51. China, W. E. (1938). "Some Homoptera new to the British list." Ent. Mon. Mag. 74: 235–44.

Includes key to the British species of *Megamelus*.

52. Smart, J. (1934). "On the biology of the black fly, *Simulium ornatum* Mg." Proc. R. Phys. Soc. Edinb. 22: 217–38.

A full account, including the description of an apparatus for rearing Simuliidae.

53. Goddard, W. H. (1938). "The description of the puparia of fourteen British species of Sphaeroceridae (Borboridae, Diptera)." Trans. Soc. Brit. Ent. 5: 235–58.

These flies were bred on several different materials, including decaying lawn-mowings, garden refuse, and the dung of cows, deer, sheep and mice.

54. Edwards, F. W. (1938). "On the British Lestremiinae, with notes on exotic species. 5 [6, 7]. (Diptera, Cecidomyiidae.)" Proc. R. Ent. Soc. Lond. B, 7: 199–210, 229–43, 253–65.

55. Rolfe, S. W. (1937). "Notes on Diplopoda. IV. The recognition of some millipedes of economic importance." J. S.-E. Agric. Coll. Wye, 40: 99–107.

56. Rolfe, S. W. (1938). "Notes on Diplopoda. V. The recognition of some millipedes of economic importance. II." J. S.-E. Agric. Coll. Wye, 42: 214–15.

(**55** and **56**.) Recognition characters and habitat notes concerning four "flat-backed" millipedes, three belonging to the family Polydesmidae and one to the Strongylosomidae; and eight "snake" millipedes, five belonging to the Iulidae and three to the Blaniulidae.

57. Lebour, M. V. (1937). "The eggs and larvae of the British Prosobranchs with special reference to those living in the plankton." J. Mar. Biol. Ass. U.K. 22: 105–66.

A summary of present knowledge of the larvae of all British Prosobranch Mollusca, with descriptions of the eggs. Full bibliography.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **3, 4, 10, 15, 41, 105, 112, 139, 152, 154, 175, 185, 186, 188**

58. Laurie, R. Douglas & Jones, J. R. Erichsen (1938). "The faunistic recovery of a lead-polluted river in north Cardiganshire, Wales." J. Anim. Ecol. 7: 272–89.

After describing the way in which pollution occurred by the oxidation of lead sulphide to lead sulphate, records are presented of surveys, giving lists of animals and amounts of lead in the water, from 1921 (when the last mine stopped working and the fauna comprised only 14 species, mostly insects) to 1937. By 1932 the recovery, shown by a list of 103 species, had permitted enough trout for fishing, and now the river is considered practically normal.

59. Pentelow, F. T. K., Butcher, R. W. & Grindley, J. (1938). "An investigation of the effects of milk wastes on the Bristol Avon." Minist. Agric. Fish., Fish. Invest. Ser. 1, 4, No. 1: 1–76. (London: H.M. Stationery Office. Price 4*s*. 6*d*.)

Pollution is less severe at Chippenham from the dried and condensed milk products than where the effluent contains whey from butter or cheese making. Indicators of pollution were increased turbidity; presence of "sewage fungus" (*Sphaerotilus natans*, *Cladothrix dichotoma*) black silt, *Asellus* and leeches; and low dissolved oxygen content. The situation was improved by putting part of the wastes through the town sewers. Methods of chemical analysis are listed with authority. Algae were studied, in part, by the glass plate method; invertebrates were collected with Percival's scoop. Species given with notes on abundance.

60. Marshall, F. H. A. (1936). "Sexual periodicity and the causes which determine it." Philos. Trans. B, 226: 423–56.

A very good general review of the field of sexual periodicity, which will be of great use to physiologists and ecologists alike. (See Review in J. Anim. Ecol. (1939) 8: 173.)

61. Rowlands, I. W. (1938). "Preliminary note on the reproductive cycle of the red squirrel (*Sciurus vulgaris*)." Proc. Zool. Soc. Lond. A, 108: 441–3.

A preliminary investigation of 388 specimens suggests that the breeding season is prolonged, the peak in male activity being in December and January, while pregnant females were obtained nearly all the year round, though details are not yet enough to show a similar peak.

62. Brambell, F. W. R. & Rowlands, I. W. (1936). "Reproduction of the bank vole (*Evotomys glareolus*, Schreber). I. The oestrous cycle of the female." Philos. Trans. B, 226: 71–97.

The breeding season is from the middle of April until the beginning of October. It is estimated that one female may rear four or five litters in a season. The mean number of foetuses *in utero* in 70 late pregnancies was 4·11. Ovulation occurs spontaneously in the absence of copulation. There is a well-marked anoestrus with vaginal closure.

63. **Rowlands, I. W.** (1936). "Reproduction of the bank vole (*Evotomys glareolus*, Schreber). II. Seasonal changes in the reproductive organs of the male." Philos. Trans. B, 226: 99–120.

Seasonal activity of the male commences early in March. Young males born early in the breeding season become sexually mature before the end of the same season. In November there is complete cessation of spermatogenetic activity.

64. **Deanesly, R.** (1935). "The reproductive processes of various mammals. Part IX. Growth and reproduction in the stoat (*Mustela erminea*)." Philos. Trans. B, 225: 458–92.

The stoat has a restricted breeding season. The young are all born in early spring, generally in April, and lactation lasts about 5 weeks. They may come into oestrus and ovulate while still lactating, but no second pregnancies were found. The reproductive cycle is, therefore, of a type hitherto undescribed. The essentials are—short effective breeding season, although the female ovulates all the year round, and the occurrence of fertile males during two-thirds of the year. The limitation may be due to a seasonal change in the pituitary.

65. **Baker, J. R. & Ranson, R. M.** (1938). "The breeding seasons of Southern Hemisphere birds in the Northern Hemisphere." Proc. Zool. Soc. Lond. A, 108: 101–41.

Contains a complete summary of records dealing with this problem. Some species show a persistence of the native rhythm, others are modified by changed external factors.

66. **Rowan, W.** (1938). "London starlings and seasonal reproduction in birds." Proc. Zool. Soc. Lond. A, 108: 51–77.

Much of the theory based on recent physiological work upon migration is questioned, particularly that dealing with the effect of light intensity. Starlings from winter roosts on London buildings were found to have enlarged gonads, though the light reaching them was negligible. The factor responsible may have been wakefulness caused by traffic.

67. **Lind, E. M.** (1938). "Studies in the periodicity of the algae in Beauchief Ponds, Sheffield." J. Ecol. 26: 257–74.

Increase in algae in 1934–5 followed spawning of frogs, probably through increased phosphates (p. 262). Brief notes on animal life are given.

68. **Raymond, C. J.** (1938). "Brown-trout geology: a comparison of trout growths and geological strata." Salm. Trout Mag. No. 93: 329–38.

Data on the rate of growth of brown trout, based on scale-readings, from 14 different waters in Great Britain and an attempt to correlate the growth rate with the geology of the various districts. No chemical data are given.

69. **Marshall, S. M., Nicholls, A. G. & Orr, A. P.** (1937). "On the growth and feeding of the larval and post-larval stages of the Clyde herring." J. Mar. Biol. Ass. U.K. 22: 245–67.

This paper also contains an account of experiments on oxygen consumption and temperature toleration.

70. **Bull, H. O.** (1938). "Studies on conditioned responses in fishes. Part VIII. Discrimination of salinity changes by marine Teleosts." Rep. Dove Mar. Lab. No. 5: 19–35.

Carefully controlled experiments with 17 species show that these fish are able to perceive small salinity changes, such as occur naturally, and will respond purposively to them.

71. **Kozhantshikov, I. W.** (1938). "Physiological conditions of cold-hardiness in insects." Bull. Ent. Res. 29: 253–62.

Cold-hardiness depends on the physiological state of the organism, e.g. insects in diapause are more hardy than insects stopped in their development, while growing insects are practically non-cold-hardy. The difference in cold-hardiness in these groups depends on the specificity of their cellular respiration. The cellular respiration of cold-hardy insects is characterized by its definite thermostable part.

72. **Brown, S. C. S.** (1938). "Mortality amongst larvae of *Stenoptilia graphodactyla*, Treits. (Lep. Pyralidina). Ent. Rec. 50: 149.

Larvae of this plume moth entering closed flowers of *Gentiana pneumonanthe* are protected from the weather; occasionally they enter expanded flowers and are likely to be drowned in trapped rain-water.

73. **Morris, S.** (1938). "The life story of *Apatura iris*." Entomologist, 71: 156–60.

Conclusion of a detailed study of the life history of this butterfly.

74. **Williams, C. B.** (1936). "The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap." Philos. Trans. B, 226: 357–89.

75. **Russell, S. G. Castle** (1938). "The third brood of *Heodes* (*Lycaena*) *phlaeas*, Linn., 1761." Ent. Rec. 50: 1–2.

The author is not convinced that a third brood of this butterfly does occur in nature in this country in any appreciable numbers. See also **T. B. Fletcher** (1938). Ent. Rec. 50: 56.

76. **Querci, O.** (1938). "Influence of reflected radiations on insects." Ent. Rec. 50: 42–3.

Larvae of the large white butterfly were confined in boxes of white paper and exposed to radiations. Temperatures attained and length of life under these conditions are briefly indicated, also the effect of wind.

77. **Cockayne, E. A.** (1938). "Notes on the life-history of *Leucania l-album*, L." Ent. Rec. 50: 13–18.

A rare immigrant moth which apparently reached the south coasts in large numbers about 1933 and has continued to breed here.

78. **Tulloch, J. B. G.** (1938). "Early swarms of bees." Entomologist, 71: 197.

There was no rain or frost during February and March 1938 at Abergavenny. The author's bees began work about 14 February; a swarm emerged on 7 April to be followed by second and third swarms from the same hive on 14 and 17 April!

79. Guichard, K. M. (1938). "*Andrena humilis* and *Picris hieracioides.*" Ent. Mon. Mag. 74: 233–4.

Andrenid bees are the primary fertilizing agents of the flowers of *Picris hieracioides.*

80. Blackburn, K. B. (1938). "Pollination of a rare Alpine plant by a Carabid beetle." Entomologist, 71: 238.

Carabus monilis observed in the Island of Rhum collecting at flowers of *Cherleria sedoides.*

81. Andrews, H. W. (1938). "Retarded emergence in Trypetidae." Ent. Rec. 50: 26–7.

Records emergence in 1937 of *Trypeta vectensis* and *Euribia spoliata* from seedheads gathered in 1935 which had already produced a batch of flies in 1936.

82. Thomson, R. C. Muirhead (1938). "The reactions of mosquitoes to temperature and humidity." Bull. Ent. Res. 29: 125–40.

The reactions of *Culex fatigans* to temperature studied by means of a new type of temperature gradient apparatus based on the same principle as the humidity alternative character. Its reactions to humidity were studied by means of the alternative chamber in a dark constant temperature room at 25° C.

83. Mellanby, K. (1938). "Diapause and metamorphosis of the blowfly, *Lucilia sericata* Meig." Parasitology, 30: 392–402.

Diapause is common in this species and is caused by overcrowding, dry meat, heat or desiccation which prevent the corpus allatum from secreting a necessary hormone. It is an advantageous arrangement by which pupation is prevented until the conditions are suitable for the more fragile adult.

84. Butler, G. C. (1938). "A further contribution to the ecology of *Aleurodes brassicae* Walk. (Hemiptera)." Proc. R. Ent. Soc. Lond. A, 13: 161–72.

Discusses parasites and predators, effects of high and low temperatures on survival and on oviposition, effect of humidity on oviposition, causes of migration and effect of various biotic and physical factors in nature.

85. Fletcher, T. B. (1938). "Early dates for grasshoppers." Ent. Rec. 50: 94.

Five species were adult unusually early in 1938 at Rodborough, Glos.

86. Harvey, L. A. (1938). "Preliminary note on the relations between grasshoppers and the recolonisation of denuded heath- and moor-land vegetation." Trans. Soc. Brit. Ent. 5: 291–7.

The distribution of several species of grasshopper has been determined in relation to burned and unburned ground in Devon. *Myrmeleotettix maculatus* occurs on the burned areas and is absent or very sparse on unburned ground. *Chorthippus parallelus* and *C. bicolor* are found in the thick vegetation of the unburned areas, and only colonize the burned ground heavily as the vegetation begins to recover and form a relatively dense cover.

87. Fox, H. M., Wingfield, C. A. & Simmonds, B. G. (1937). "The oxygen consumption of Ephemerid nymphs from flowing and from still waters in relation to the concentration of oxygen in the water." J. Exp. Biol. 14: 210–18.

There is an extreme contrast between *Cloëon dipterum* and *Baëtis* sp. in the relation between oxygen consumption and oxygen concentration in the water. A relation exists between oxygen consumption and size of animal, for instance, the oxygen consumption of the larger species *Leptophlebia marginata* is lower than that of the smaller species *L. vespertina*.

88. Anon. (1938). "The possibility of improving Scotch lochs." Game and Gun, 15: 328.

The acid lochs of Scotland are unsuitable for the common shrimp (*Gammarus pulex*), which, however, was believed to thrive in fresh water of Ireland. Samples of shrimp from lochs having a wide range of *p*H contained almost entirely *G. duebeni*, usually found in brackish water. Its possible importation as a food for Scotch trout is discussed.

89. Thomas, H. Dighton (1937). "Fossils and their original environment." S. East Nat. 42: 46–64.

A demonstration of the existence and action, in the palaeontological history of marine faunas, of exactly the same environmental control as is found in the study of living marine animals.

90. Moore, Hilary B. (1937). "A comparison of the biology of *Echinus esculentus* in different habitats. Part III." J. Mar. Biol. Ass. U.K. 21: 711–19.

Seasonal changes in gonad volume in sea urchins from Plymouth compared with those from Port Erin. The mean size of sea-urchins increases towards the south. Comparison is made between specimens from Millport, Port Erin, and Plymouth. The pigments present in sea-urchins appear to be derived from the food. A diagram is given of the seasons of shell and gonad growth, spawning, etc., at Plymouth.

91. Moore, Hilary B. (1937). "The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality." J. Mar. Biol. Ass. U.K. 21: 721–42.

92. Wilson, D. P. (1937). "The influence of the substratum on the metamorphosis of *Notomastus* larvae." J. Mar. Biol. Ass. U.K. 22: 227–43.

An account of experiments to show that the larvae of *Notomastus latericeus* Sars, a mud-dwelling Polychaete, exercise some choice of the soil on which they settle. It is pointed out that such choice, if general, would have important bearings on distribution problems.

93. Graham, M. (1938). "Phytoplankton and the herring. Part III. Distribution of phosphate in 1934–1936." Minist. Agric. Fish., Fish. Invest. Ser. 2, 16, No. 3: 1–26. (London: H.M. Stationery Office. Price 2*s*.)

Includes 15 charts of horizontal and vertical stratification of phosphate in the North Sea. Success of *Rhizosolenia* (which may interfere with herring fishing) is influenced not only by a strong Atlantic influx of nutrient salts, but probably by a complex of factors associated with the influx.

94. Jenkin, P. M. (1937). "Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel." J. Mar. Biol. Ass. U.K. 22: 301–43.

A full account of experiments on the relation of photosynthesis to energy in the sea. The cultures of diatoms were exposed to light at various depths. A method is described for calculating the available energy at any depth in Joules or g. cals.

95. Atkins, W. R. G. & others (1938). "Measurement of submarine daylight." J. Cons. Int. Explor. Mer, 13: 37–57.

In this report of an international committee suggestions are made of a standard method for the measurement of light intensity by a photoelectric cell. Errors and necessary corrections are discussed and practical advice given for the construction of apparatus and its use at sea. An electrical transparency meter is also described.

96. Fox, H. M. & Wingfield, C. A. (1938). "A portable apparatus for the determination of oxygen dissolved in a small volume of water." J. Exp. Biol. 15: 437–45.

Only 1–2 c.c. of water are required for the estimation, and the method is accurate to 2%.

97. Gunn, D. L. & Kennedy, J. S. (1936). "Apparatus for investigating the reactions of land Arthropods to humidity." J. Exp. Biol. 13: 450–9.

4. PARASITES

See also **84, 128, 153**

98. Mayfield, R. B. (1938). "Rat-fleas in Plymouth." Parasitology, 30: 314–19.

Seventy-seven rats (*Rattus norvegicus* and *R. rattus*) were trapped in an isolated part of the docks and six in the town. On both groups the fleas *Nosopsyllus fasciatus* and *Leptopsylla segnis* were found, and in the dock group *Xenopsylla cheopis* was common. The collection was made over three years and seasonal variations are discussed though the data are admittedly scanty.

99. Buxton, P. A. (1938). "Studies on populations of head-lice (*Pediculus humanis capitis*: Anoplura). II." Parasitology, 30: 85–110.

Using 2000 hair crops collected from Africa, Ceylon and Palestine, detailed data have been obtained on the relation of the head lice count to the race, sex, age and weight of hair of the host individual and to the season of the year. As these relationships may be bound up with local or racial customs the investigations could be extended most profitably by people who are well acquainted with the localities.

100. Leiper, J. W. G. & Clapham, P. A. (1938). "Some Nematode parasites found in Chinese water deer (*Hydropotes inermis*), with a description of *Trichostrongylus cevarius* n.sp." J. Helminth. 16: 77–82.

Viscera of 24 water deer bred in Whipsnade Park were examined and 14 species of Nematode newly recorded. All except three of these are such as are common to the district. A new species, and two species of *Ostertagia* (*O. lyrata* and *O. gruhneri*) have not been recorded in England before. Probably these are natural parasites of the deer in China and came over with the original stock.

101. Clapham, P. A. (1938). "New records of helminths in British birds." J. Helminth. 16: 47–8.

These records show that the host range of many helminth species is considerably wider than had been suspected.

102. Clapham, P. A. (1938). "Are there host strains within the species of *Syngamus trachea*?" J. Helminth. 16: 49–52.

The view that physiological strains of the gapeworm become so adapted to one species of host that they cannot infect another is discounted by experiments in which this parasite has been transmitted to chickens and pheasants from rook, crow, jackdaw, magpie, jay, starling, and turkey strains. The infection was not direct, but via earthworms as intermediate hosts. Larvae remain infective in earthworms for up to 3½ years and this is probably the normal method of transmission of the disease.

103. Davies, T. I. (1938). "A description of *Hymenolepis neoarctica* n.nom., syn. *H. fusus* Linton, 1927, with a discussion on the synonymy of *Taenia fusus* Krabbe, 1869." Parasitology, 30: 339–43.

Strobilae of *H. neoarctica* and *H. ductilis* were found in the intestine of a greater black-backed gull (*Larus marinus*) shot near Aberystwyth. This is the first record for these species in the Old World and presents evidence of a Neoarctic element in the Cestode fauna of British gulls.

104. Thompson, G. B. (1938). "The parasites of British birds and mammals. XXI. Additions and corrections to previous contributions." Ent. Mon. Mag. 74: 277–9.

Forty-seven British species of fleas are now known.

105. Thompson, G. B. (1938). The parasites of British birds and mammals. XX. The ectoparasites of the house-martin, swift, swallow and sand-martin." Ent. Mon. Mag. 74: 147–51.

Nine species of biting lice have been recorded from these four birds, but only four are found frequently. The sand martin possesses a flea specific to itself, the house martin four specific species; the swallow and swift are almost free. The house martin is the only species parasitized by *Oeciacus hirundinis*, resembling a "bed-bug". In the British Isles the house martin and swift are parasitized by two species of Hippoboscid flies.

106. Davies, T. I. (1938). "Some factors governing the incidence of Helminth parasites in the domestic duck." Welsh J. Agric. 14: 280–7.

The nature of the geological information is responsible for determining the type of the prevalent species of parasite, e.g. flukes, are present in areas where the supply of natural lime allows a large population of fresh-water snails, but are absent where the surface waters are lime deficient. Rapid flowing streams dispose of helminth eggs and hinder the increase of colonies of the invertebrate secondary hosts.

107. Williams, G. (1938). "On the occurrence of *Scopelocheirus hopei* and *Cirolana borealis* in living *Acanthias vulgaris* (spiny dogfish)." Irish Nat. J. 7: 89–91.

The Amphipod parasite, *S. hopei*, was found in a number of living dogfish, destroying vulnerable soft tissues such as the gills, eye muscles and associated nerves. The optic nerves in each case remained uninjured. From 4 to 12 specimens were taken from each host. The occurrence of the Isopod *C. borealis* in Irish waters both as a free-living form and as a parasite on the dogfish is also recorded.

108. Baylis, H. A. (1938). "On two species of the Trematode genus *Didymozoon* from the mackerel." J. Mar. Biol. Ass. U.K. 22: 485–92.

The author gives reasons for dividing the former species *D. scombri* into two species, *scombri* and *faciale*. The first is found in cysts in the roof of the pharynx of the mackerel, the second behind the eye. A full description of *D. faciale* is given.

109. Christison, M. H., Mackenzie, I. & Mackie, T. J. (1938). "*Bacillus salmonicida* bacteriophage: with particular reference to its occurrence in water and the question of its application in controlling *B. salmonicida* infection. A report to the Fishery Board for Scotland." Fisheries, Scotland, Salmon Fish., 1938, No. 5: 1–18. (Edinburgh: H.M. Stationery Office. Price 1*s*.)

This phage may occur in winter or summer in waters infected or uninfected with furunculosis, and does not always occur in infected waters. It is widespread and of no value as an indicator of the disease. It had no inhibitory action on the course of epizootics among brown trout in tanks. Bacteriological technique fully described.

110. Salt, G. (1938). "Experimental studies in insect parasitism. VI. Host suitability." Bull. Ent. Res. 29: 223–46.

Host may be found and accepted, but not suitable because the attack is frustrated (i.e. host unsuitable for adult parasitoid) by host escaping attack; by host resisting actively or passively; and by host inhibiting oviposition. The parasitism may also be unsuccessful (i.e. host unsuitable for developing parasitoid) because host is physically unsuitable, e.g. in size, in texture, etc.; or because host is chemically unsuitable either as an environment or as food; or because host is biologically unsuitable, e.g. host dies, moves, moults, etc.

111. Bisset, G. A. (1938). "Larvae and pupae of Tachinids parasitizing *Pieris rapae* and *P. brassicae* L." Parasitology, 30: 111–22.

Larvae and pupae of these two species of *Pieris* were found to contain *Phryxe vulgaris, P. nemea, Epicampocera succincta, Compsilura concinnata,* and an unknown species which is described.

112. Cameron, E. (1938). "A study of the natural control of the pea moth, *Cydia nigricana*, Steph." Bull. Ent. Res. 29: 277–313.

Includes a comprehensive account of three parasites: *Ascogaster quadridentatus* (Braconid), *Glypta haesitator* (Ichneumonid) and *Angitia* sp. (Ichneumonid). The apparent significance of rainfall, sunshine and temperature on the moth's distribution in England is discussed.

113. Nixon, G. E. J. (1938). "A preliminary revision of the British Proctotrupinae (Hym., Proctotrupoidea)." Trans. R. Ent. Soc. Lond. 87: 431–66.

A study of an important group of parasitic Hymenoptera. Includes keys, many figures, distributional and host records.

114. Cole, H. A. (1938). "On some larval Trematode parasites of the mussel (*Mytilus edulis*) and the cockle (*Cardium edule*). Part II." Parasitology, 30: 40–3.

Describes a new cercaria *C. cambrensis* which infects all cockles collected from the Menai Straits. Its structure is very like that of a metacercaria found by Jameson in the mantle of mussels and thought to give rise to the pearl-inducing Trematodes. It may be an earlier stage of the same form. The pearl-inducing Trematode is common in mussels collected in this same locality.

5. FOOD AND FOOD-HABITS

See also **6, 10, 17, 26, 27, 31, 34, 36, 39, 69, 84, 88, 130, 134, 147, 151, 155, 157, 158**

115. Austin, M. D. & Rolfe, S. W. (1938). "The grey squirrel: a review of the present situation." J. S.-E. Agric. Coll. Wye, 42: 93–8.

A review article which includes a tabulated list showing the wide range of food consumed.

116. Elmhirst, R. (1938). "Food of the otter in the marine littoral zone." Scot. Nat.: 99–102.

The presence of otters on the shore is indicated by defaecation mounds often surrounded by bright green vegetation and used for generations. Remains of mammals, birds, fish, Crustacea (eight species) and rarely molluscs, have been found in the faeces and in places frequented. There are notes on habits of otters and the type of shore frequented by them.

117. Ford, J., Chitty, H. & Middleton, A. D. (1938). "The food of partridge chicks (*Perdix perdix*) in Great Britain." J. Anim. Ecol. 7: 251–65.

Crops of 69 chicks, mostly from hay, lucerne, etc., not from grain fields, showed that animal food predominates in the first two weeks, decreases by half at the end of the third week, and gives way to almost entirely plant food after three weeks.

118. Carpenter, G. D. H. (1937). "Bird as enemies of butterflies." S. East Nat. 42: 93–5.

A statement of the importance to the theory of mimicry of the question whether birds do or do not eat butterflies, and an invitation to amateur naturalists to co-operate in the work of answering it.

119. Anon. (1937). "Garden birds." J. Minist. Agric. 43: 1026–8.

Food habits of blackbird, song thrush, robin, dunnock (hedge sparrow) and wren.

120. Chitty, D. (1938). "A laboratory study of pellet formation in the short-eared owl (*Asio flammeus*)." Proc. Zool. Soc. Lond. A, 108: 267–87.

Experiments show that a fairly constant relationship exists between the time for pellet formation and the amount of the meal. Quantitative data on food consumed suggest that about $2000 \pm 50\%$ voles (*Microtus*) may be taken in a year. In an area on the Scottish border in April 1933, when a vole census was done concurrently with one of short-eared owls, the toll would represent 0·02 to 0·05% of the population daily.

121. Anon. (1937). "Interesting birds: (1) The barn owl." J. Minist. Agric. 43: 1124–5.

Remarks on food habits. Further references in J. Minist. Agric. 44: 6 (nightjar), 108–9 (kestrel), 204 (blackbird), 310–11 (song-thrush), 421 (robin), 519 (wren), 612–13 (long-tailed tit), 722–3 (spotted flycatcher), 830 (lapwing).

122. Deane, C. Douglas (1938). "Observations on the rook." Bird Notes and News, 18: 17–19.

There is a brief mention of pellet-casting in this species. In the neighbourhood concerned (Co. Down) they consisted mostly of grain with pieces of turnip and potato. At one nest they consisted almost entirely of burying beetles.

123. Glegg, W. (1938). "Birds taking rubber articles." Essex Nat. 26: 26–9.

A résumé of previous evidence on this subject is given together with new observations. Rooks, terns, gulls, starlings, puffins, and possibly carrion crows are involved. No significant choice of colour is noticed. The articles may be mistaken for food or swallowed to aid digestion.

124. Embry, B. (1938). "Isle of Wight and the seven toads: a sugaring experience. Entomologist, 71: 274.

Toads attacking moths attracted to sugar.

125. Neill, R. M. (1938). "The food and feeding of the brown trout (*Salmo trutta* L.) in relation to the organic environment." Trans. Roy. Soc. Edinb. 59: 481–520.

A study carried out on the river Don, in Aberdeenshire. The author comes to the following conclusions: (1) trout feed on the whole range of animals present, (2) the choice of food is governed by accessibility only, and hence, (3) the *quality* of food is not a limiting factor in the distribution of the brown trout. Lists are given of the flora and fauna of the region under observation.

126. Tchernavin, V. (1938). "The absorption of bones in the skull of salmon during their migration to rivers." Fisheries, Scotland, Salmon Fish. 1938, No. 6: 1–4. (Edinburgh: H.M. Stationery Office. Price 6*d*.)

The main bones of the jaw, palatines, vomer and supra-ethmoid increase their size at the expense of calcium from bones forming the gill-covers, the branchiostegals and postorbitals as well as from the scales. In fact jawbones and teeth, useless to a fasting fish, grow at the expense of certain essential bones.

127. Whitney, R. J. (1938). "A plague of the beetle *Harpalus rufipes* Degeer." Ent. Mon. Mag. 74: 200–1.

"The beetles have evidently become conspicuous because, owing to the disturbance of their normal food supply, they now collect near the houses from the barren fields. How far this is related to the recent discontinuance of potato crops in the vicinity, it is not possible to say."

128. Murray, J. (1938). "The red spider and its prey." Northw. Nat. 13: 28.

The scarlet mite, *Anystis baccarum*, was twice noticed to attack a thrips (*Physothrips vulgatissimus*) and a moth fly (*Psychodes* sp.). Its presence in henhouses may be beneficial if it feeds on the various insect parasites of the birds.

129. Moore, H. B. (1938). "Algal production and the food requirements of a limpet." Proc. Malacol. Soc. Lond. 23: 117–18.

A study of limpets (*Patella vulgata*) living on an alga-covered wall. The areas eaten are plotted against the volumes of the limpets responsible, and show an approximately linear relationship.

6. POPULATIONS

See also **35, 39, 40, 41, 60–6, 83, 90, 91, 93, 99, 108, 110, 120, 169, 177, 184–8**

130. Fenton, E. Wyllie (1938). "Biological notes for 1937." Scot. J. Agric. 21: 74–81.

A remarkable increase of rabbits in 1937; badgers also increasing in numbers and in extent of range. Blackbirds in the dry summer changed from their habits of turning over dead leaves and material on the ground to uprooting plants in order to get grubs. The younger generation learned this new habit and kept to it. Mass movements and temporary increase in numbers of the antler moth causing special damage to moor mat grass (*Nardus stricta*) and the rushes (*Juncus squarrosus*).

131. Anon. (1938). "The stock-carrying capacity of hill grazings in Scotland—I-II." Scot. J. Agric. 21: 219–32, 345–63.

The decline in sheep stocks in the Highland counties has been largely due to the establishment of deer forests. Other factors involved are bracken, unbalanced grazing by sheep, heather, drainage and removal of lime and phosphates, etc., and damage by rabbits and mountain hares. Figures of the numbers of sheep in Argyll, Inverness, Perth, Ross and Cromarty and Sutherland since 1855 to date are given.

132. Middleton, A. D. (1937). "Whipsnade Ecological Survey, 1936–7." Proc. Zool. Soc. Lond. A, 107: 471–81.

A preliminary survey of the animals living in a wild or semi-wild state at Whipsnade including population counts. Since 1933 wallabies (*Macropus*) have remained stationary. Chinese water deer (*Hydropotes inermis*) have fluctuated greatly and have been reduced once by an epidemic, while muntjac deer (*Muntiacus muntjac*) have remained at the initial level. Some figures are also given for rabbits, rats, squirrels and continental dormice (*Glis*).

133. Matheson, C. (1938). "Weights of brown and black rats." Naturalist, Lond. No. 980: 251–3.

Weight distribution of brown rats from the official rat-catching returns of Cardiff. Fewer data are available for the black rat. In both species information is needed on the sex ratio.

134. Moon, J. H. (1938). "Mortality among mute swans on Ullswater." Northw. Nat. 13: 25.

Every swan that takes up its abode on Ullswater dies. During the past three years thirteen swans which have died in this way have been examined. The food contents were unidentifiable but in every case lead was found in the tissues. Some food plant may be responsible both in this case and in that of the mortality of whooper swans on Loch Dochart. A. A. Dallman suggests *Lobelia dortmanna* as a possible cause.

135. Huxley, J. S. (1938). "Nests and broods in Whipsnade sanctuary in two successive years." Proc. Zool. Soc. Lond. A, 108: 445–52.

A number of tables and figures show how the year 1937, being less favourable than its predecessor, exerted an effect upon total nests, nests occupied, the number in which hatching took place, the size of clutch, the number of young hatched and the number of young fledged.

136. Fisher, J., Stewart, M. & Venables, L. S. V. (1938). "Gannet colonies of Shetland." Brit. Birds, 32: 162–9.

A description, census (2045 pairs) and history of the Hermaness colony.

137. Vevers, H. G. & Fisher, J. (1938). "The 1938 census of gannets (*Sula bassana*) on Ailsa Crag." J. Anim. Ecol. 7: 303–4.

On some parts there has been an increase, on others a decrease, with a net over-all decrease of 9·4% since 1937.

138. Fisher, J. & Venables, L. S. V. (1938). "Gannets (*Sula bassana*) on Noss, Shetland, with an analysis of the rate of increase of this species." J. Anim. Ecol. 7: 305–13.

The colony is described, and relations with other birds noted. The analysis, made after consultation with J. B. S. Haldane and C. F. Fisher, is presented with a graph of the theoretical and actual increase. It shows that the increase from one pair in 1914 to 1518 pairs in 1938 is due to colonization as well as to breeding up to certainly 1935.

139. Kemp, S. (1938). "Oceanography and the fluctuations in the abundance of marine animals." Nature, Lond. 142: 777–9 and 817–20.

The annual, restricted, fluctuations are masked by long-term fluctuations. At Plymouth there has been a decline in the numbers of young fishes since 1931, correlated with a decrease in phosphate in the water, apparently due to change in water movements off the Atlantic mouth of the Channel, leading to a shortage of mixed Atlantic ("*elegans*") water. There is no correlation of these phenoména with temperature or salinity observations in the Channel, but there is evidence of long-term fluctuations from Norway and from West Greenland, which are apparently due to changes in temperature. The author calls attention to the need for a fuller hydrographic investigation of the eastern Atlantic, and to the fact that, with certain exceptions, the scientific administration of fisheries in the British Empire is either deficient or lacking.

140. Farran, G. P. (1937). "The herring fisheries off the north coast of Donegal." J. Dep. Agric. Saorstát Éireann [Éire], 34: 262–70.

Summary of the Department's work from 1921–35. Explanation of the use of population analysis for forecasting a season's catch. Unfortunately, the life history is not known before herring join the shoal (usually at 3–4 years). Maximum age reached is 12 years.

141. Farran, G. P. (1938). "On the size and number of the ova of Irish herrings." J. Cons. Int. Explor. Mer, 13: 91–100.

Distinction between spring and autumn spawners from size of ova in relation to weight of gonad.

142. Hickling, C. F. (1938). "The English plaice-marking experiments 1929-32." Minist. Agric. Fish., Fish Invest. (1937), Ser. 2, 16, No. 1: 1–80. (London: H.M. Stationery Office. Price 4*s*.)

19,684 plaice were marked between 1929 32 and 6750 were recaptured, five in the sixth year after release. There is a rough general rate of decrease of 70% per annum. Distribution from marking stations off the Dutch, German and Danish coasts is shown on maps. A useful system of weighted contouring is used to make allowance for the seasonal difference in chance of recapture by fishing vessels. Considerable mixing of stocks has occurred, being at its greatest after one year. In winter, while English steam trawlers make wide cruises, the contribution of fish recaptured by other nationalities is small and largely from the coast. Since the faster growing plaice move offshore their inclusion in greater numbers in the spring and summer samples affects to an unknown extent the graph showing growth rate: which, however, does seem to be greatest just then. Returns of the smallest sizes are least frequent probably because they are not marketable and are thrown back. There is some evidence that the fishing practice of Denmark with short period seine hauls may prevent excessive deaths among these rejected fish.

143. Robertson, J. A. (1938). "The sprat and the sprat fishery of England." Minist. Agric. Fish., Fish Invest. Ser. 2, 16, No. 2: 1–100. (London: H.M. Stationery Office. Price 4*s*. 6*d*.)

Sprat fishing is carried out on a small, local scale from lightly equipped boats operating in territorial waters. The number of localities engaged in the trade is only a small part of those that might be developed. There is considerable fluctuation in the landings, particularly in Norway, much less in Britain; but there is no general correspondence between different countries. Norway has a virtual monopoly of the imports, which have fetched £6. 13*s*. per cwt. compared with only 3 to 16*s*. paid for British landings. The British canning industry might profitably be expanded; but as the sprat is taken as a winter immigrant the seasonal nature of the trade is an objection. Statistics of age-composition and length-frequency from scale analysis are given, without any summary. The English and Norwegian fisheries depend chiefly on immature yearlings, which, though of the same year class, are taken younger in Norway as the season opens in May. Copepods are the main food. Technique of fat extraction is given: the yield is good (14–20%) at the season's start, dropping to 5–7% at the end. Parasites were *Lernaeenicus sprattae* on 46 out of 62 fish, *L. encrasicola* on 15, both species on one only (though the former sticks on the eye, the latter on the body).

144. **Russell, F. S. (1937).** "The seasonal abundance of the pelagic young of Teleostean fishes in the Plymouth area. Part IV. The year 1936, with notes on the conditions as shown by the occurrence of plankton indicators." J. Mar. Biol. Ass. U.K. 21: 679–96.

Russell, F. S. (1938). "On the seasonal abundance of young fish. V. The year 1937." J. Mar. Biol. Ass. U.K. 22: 493–500.

A comparison with the reports of previous years (1930–5). In both 1936 and 1937 there were very small numbers of *Sagitta elegans*, and, correlated with this, there was a complete absence of the usual peak of young spring spawners.

145. **Graham, M. (1938).** "Rates of fishing and natural mortality from the data of marking experiments." J. Cons. Int. Explor. Mer., 13: 76–90.

A simplified mathematical discussion of the planning and use of marking experiments on fish.

146. **Éire, Dep. Agric., Fish. Branch [1938].** "Statistics of salmon, sea trout and eels captured during each of the years 1937, 1935, 1933, 1931, 1929, 1927." Pp. 1–19. (Government Publications Sale Office, 3–4 College St., Dublin. Price 4*d.*)

Tables without discussion.

147. **Macfarlane, P. R. C. (1938).** "Salmon of the upper Solway district 1934." Fisheries, Scotland, Salmon Fish. 1938, No. 3: 1–18. (Edinburgh: H.M. Stationery Office. Price 1*s.*)

Examination of 1890 sets of scales from nets set near the mouth of the River Annan showed that the fishery depends chiefly on grilse and small summer fish (79%). Previously spawned fish (1·1%) were in the lowest proportions yet found. 88% of the smolts had migrated when two-years old, thus giving a low average age, as expected from the low latitude. The calculated lengths of smolts were equal to the highest previously found (River Nith). Of the three neighbouring rivers, Annan, Nith and Dee, feeding conditions are inferior in the latter. This probably accounts for the smaller average length and higher average age at migration observed in the Dee smolts.

148. **Hartley, G. W. (1938).** "Salmon caught in the sea—West Sutherland, 1937." Fisheries, Scotland, Salmon Fish. 1938, No. 2: 1–21. (Edinburgh: H.M. Stationery Office. Price 1*s.* 3*d.*)

Grilse formed 72% of the catch; spring fish 13% (only 2·5% in 1936 and unusually plentiful for a west coast fishery); small summer fish 12%; previously spawned fish less than 2% (unusually scarce). Smolt ages were: 2-year 64%; 3-year 34%. Condition of the three-year-old smolts was generally better than that of the two-year-old, a reversal of 1936 conditions.

149. **Hutton, J. A. (1938).** "Wye salmon. Results of scale-reading, 1937." Salm. Trout Mag. No. 90: 49–72.

Statistics of the number, weight and age of salmon caught by rods and nets in the River Wye in 1937. The total catch was 3568 fish weighing 62,661½ lb. Scales of 991 fish were examined for age determination. All classes were present, but large springers, i.e. those which had spent three years in the sea, predominated. Graphs showing the annual variations in catch since 1905 are included.

150. Nall, G. H. & Macfarlane, P. R. C. (1938). "Sea trout of the river Carron and Loch Doule (Dhughaill), Western Ross-shire; with an appendix on Salmon from the same river." Fisheries, Scotland, Salmon Fish. 1938, No. 4: 1–42. (Edinburgh: H.M. Stationery Office. Price 2*s*. 6*d*.)

1811 sets of scales were obtained from captures by rod and for marking work. Percentage migrating after two, three and four years of parr life and lengths of smolts at migration were: 2-year 26%, av. 16·5 cm.; 3-year 63%, av. 18·7 cm.; 4-year 10%, av. 21·3 cm. In the first winter after migration (i.e. as whitling) only 2% spawned; in the second winter 61%; in the third 34%. Sea trout, unlike salmon, seldom fail to spawn in successive years. One fish had 11 spawning marks. Carron sea trout stand high among the slower growing Scottish types which the physiography of the west coast tends to produce.

151. Allen, K. R. (1938). "Some observations on the biology of the trout (*Salmo trutta*) in Windermere." J. Anim. Ecol. 7: 333–49.

Trout caught in a seine net from the upper three metres along the shore at all seasons from November 1933 to October 1935 furnish the basis for a detailed study of growth, the age at which trout enter the lake, their condition, their food at different seasons, and an estimate of the total numbers, by ages, in the littoral region.

152. Allen, K. R. (1938). "Deterioration of Windermere trout. An attempt at an explanation." Salm. Trout Mag. No. 91: 152–6.

From a consideration of the numbers, ages, growth and mortality rates, the food and predators of the present stock of trout in Windermere it is concluded that the alleged deterioration of the trout fishery during the last 30 years cannot be ascribed to unfavourable conditions in the lake. It is suggested that the cause must be sought in the streams to which the fish go to spawn and where they spend the first year or two of their lives.

153. Laing, J. (1938). "Host-finding by insect parasites. II. The chance of *Trichogramma evanescens* finding its hosts." J. Exp. Biol. 15: 281–302.

The rate at which the parasite found the host eggs varied inversely with its distance from them.

154. Ford, J. (1938). "Fluctuations in natural populations of Collembola and Acarina. Part 2." J. Anim. Ecol. 7: 350–69.

An analysis of the way in which the numbers of very small animals in a small habitat (a small ecosystem) fluctuate in relation to environmental changes and other causes. The age distribution of the spring-tail (*Pseudachorutes subcrassus*) was analysed during increase and decrease in numbers, and the variation in its distribution throughout the habitat was compared with fluctuations in numbers.

155. Meikle, A. A. & Macfarlan, J. (1938). "Damage to pasture by the larvae of the bracken-clock." Scot. J. Agric. 21: 183–5.

Larvae of *Phyllopertha horticola* at a density of nearly 435,000 to the acre completely destroyed the turf over two acres. Birds had added to the damage by tearing up the turf.

156. Roebuck, A. (1938). "Beetles in a church." Ent. Mon. Mag. 74: 209.

Includes average daily counts of *Xestobium rufo-villosum* (death-watch beetle) for various periods between 6 April and 8 June 1938.

157. Cameron, A. E. (1938). "The antler moth on Scottish hill-pastures." Scot. Nat.: 125–7.

Infestations are confined to hill pastures, and the first indications are often given by the presence of flocks of insectivorous birds attracted by the larvae. The final ecdysis is followed by mass migration of larvae, rarely down hill, in which many are drowned in hill streams and drains. This checks the infestation. Experimental investigations indicate that many of the surviving larvae are destroyed by bacterial disease.

158. Pickles, W. (1938). "Populations, territories and biomasses of ants at Thornhill, Yorkshire, in 1937." J. Anim. Ecol. 7: 370–80.

This is the third year of the survey of ants' nests on the same area to determine the increase or decrease of nests, of ants, by number and also by live weight (biomass), and population densities. The surveys for 1935 and 1936 were described in J. Anim. Ecol. (1936) 5: 262–70, and (1937) 6: 54–61, respectively.

159. Donisthorpe, H. (1938). "Observations on a colony of *Acanthomyops* (*Dendrolasius*) *fuliginosus*, Latr., for 23 years." Ent. Rec. 50: 73–6.

The establishment of this colony was observed in 1915, since when 45 named species of myrmecophiles have been found in it.

160. Morley, B. D. W. (1938). "Some observations on a mixed *Acanthomyops* (*Dendrolasius*) *fuliginosus*, Latr., *Acanthomyops* (*Chtonolasius*) *mixtus*, Nyl., colony." Ent. Rec. 50: 94–5.

Brief account of relations between these two species of ants. The belief is expressed that the *A. mixtus* element will die out since their numbers are relatively so few.

161. Boycott, A. E. & Oldham, C. (1938). "A contagious disease of *Helix aspersa*." Proc. Malacol. Soc. Lond. 23: 92–6.

Breeding experiments on individuals infected with a disease producing greying and wrinkling of the shell.

162. Russell, F. S. (1938). "The Plymouth offshore medusa fauna." J. Mar. Biol. Ass. U.K. 22: 411–39.

An account of the fluctuations in numbers and ratios of species of medusae obtained from weekly plankton hauls during the years 1930–7, together with ecological and morphological notes on certain species. The possibility of using some of the species as indicators is discussed.

163. Hardy, A. C. (1938). "Estimating numbers without counting." Nature, Lond. 142: 255–6.

Describes a method of estimating the number of organisms where only one or two species are present by visual comparison of the sample with a specially prepared chart. Very rapid estimations can be made with an accuracy of $\pm 15\%$.

164. Lowndes, A. G. (1938). "The density of some living aquatic organisms." Proc. Linn. Soc. Lond. 62–73.

An accurate method of determining the density of living aquatic organisms is described.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **16, 35, 47, 70, 77, 84, 93, 100, 115, 127, 130, 142, 145, 150, 151, 157, 186**

165. Robinson, H. W. (1938). "Recovery of ringed puffins in Orkney where marked." Scot. Nat.: 150.

Special rings are used, the overlapping kind being useless against the birds' beaks. Owing to a scarcity of these rings, preference in ringing was given to previously marked birds, of which 28 were recaptured.

166. Hendy, E. W. (1937). "Spring migration of swallows in south-west England." Discovery, 18: 336–8.

Observations on the spring migration routes of swallows made during the years 1934–7 by observers of the Bird-watching and Preservation Societies of Devon and Cornwall. The results favour the idea of definite routes rather than broad-front migration.

167. Green, J. T. & Flintoff, R. J. (1938). "Rookeries and roosts, and the desertion of rookeries. An ecological study." Northw. Nat. 13: 148–56.

In 1928 two large rookeries in Yorkshire were suddenly deserted in the middle of the breeding season though everything remained normal in other closely located rookeries. Carrion crows can hardly be held responsible for this desertion, as notes on the rookeries kept during the subsequent ten years show that crows, though common visitors, do not drive the rooks from their nests.

168. Russell, E. S. (1937). "Fish migrations." Biol. Rev. 12: 320–37.

Migrations usually involve a movement of mature fishes upcurrent to breed, followed by a dispersion of the spent fishes downcurrent which may develop into a definite feeding migration. The whole cycle tends to keep the species in its ecological norm. Marking experiments on cod, plaice and salmon are reviewed, with maps to illustrate these principles.

169. Ford, E. (1938). "Progress in fisheries research." Sci. Progr. 33: 63–5.

Brief review of (1) transplantation of fish species to new habitats, (2) the artificial propagation of plaice-flounder hybrids in Norwegian waters, (3) data on the growth rate of lobsters, and (4) data on variation in brood size from year to year in mackerel.

170. Menzies, W. J. M. (1938). "The movements of salmon marked in the sea. III. The island of Soay and Ardnamurchan in 1938." Fisheries, Scotland, Salmon Fish., 1938, No. 7: 1–9. (Edinburgh: H.M. Stationery Office. Price 1*s*. 3*d*.)

On the south shore of Skye 94 salmon were marked and released. Of the 22 recaptures 18 were on the north and east coasts of Scotland, only four on the west. Times of arrival fell into two groups on the east coast suggesting alternative routes east and west of the Outer Hebrides. Fish marked 25 miles farther south were recaught much more locally. However, of the 35 grilse (mostly) retaken out of 280 marked, three turned up in Ireland, one in Wales. This suggests that the station was on the fringe of the migration route passing south of the Outer Hebrides to the Irish, Welsh and west of England rivers.

171. "Piscator Senior" (1938). "Migrations of European salmon: results of Scottish and Norwegian markings." Salm. Trout Mag. No. 93: 288–99.

A useful popular account of the migrations of European salmon in the sea, based on the results of marking experiments carried out by the Scottish Fishery Board and by Knut Dahl in Norway. The conclusion is reached that the feeding grounds of the salmon are situated some distance to the west of the British Isles.

172. Calderwood, W. L. (1938). "Salmon towers. A new type of salmon pass in the Doon district." Salm. Trout Mag. No. 90: 29–36.

An unusual structure to enable salmon to surmount a dam, of unstated height, on the river Doon, Ayrshire.

173. Hardy, A. C. & Milne, P. S. (1938). "Studies in the distribution of insects by aerial currents. Experiments in aerial tow-netting from kites." J. Anim. Ecol. 7: 199–229.

An application of the marine plankton net to the collection of insects between 150 and 1945 ft. above the ground, mostly at Hull. The net, attached to a kite line, was opened and closed by an arrangement of strings released by the action of acid on copper wire, the time being controlled by the strength of the acid. Meteorological observations are given, and lists of the numerous insects collected at each height.

174. Grant, K. J. (1936). "The collection and analysis of records of migrating insects, British Isles, 1931–1935." Entomologist, 69: 125–31.

175. Wiltshire, E. P. (1938). "Notes on the winter flight, in mild climates, of vernal and autumnal moths." Ent. Rec. 50: 144–6.

Compares behaviour in England and Central Europe (cold winter, short summer); Taurus, Inner Syria, Kurdistan, etc. (cold winter, long summer); coasts of Cyprus, Syria and Palestine (mild winter, long summer).

176. Nicholson, C. (1938). "Further notes on *Danaus plexippus* L. in the British Isles." Entomologist, 71: 217–25.

Records 30 new appearances of this immigrant butterfly since 1935. Further reference in **E. Bolton King**, Entomologist, 71: 236.

177. Walker, J. J. (1938). "The comma butterfly, *Polygonia c-album* (Linn.): its decadence and revival as a British insect." Trans. Soc. Brit. Ent. 5: 281–90.

A summary of its occurrences during the long period of its eclipse over the greater part of its range in old times—omitting the records from Wales and the western English counties, where the insect held its own most successfully during those critical years—with a brief account of its progressive increase in numbers and extension of range from the year 1921 onwards.

178. Harrison, J. W. H. (1938). "*Plusia gamma* in the Isle of Muck in 1938." Entomologist, 71: 183.

This moth is a migrant species.

179. Fisher, K. (Grant, K.) (1938). "Migrations of the silver-Y moth (*Plusia gamma*) in Great Britain." J. Anim. Ecol. 7: 230–47.

This moth appears to be a migrant from the Continent, analogous to swallows and many other birds. Information collected by the author and received from the Insect Immigration Committee shows that this moth arrives in summer, breeds, and migrates south in the autumn. Maps and charts of seasonal distribution and migration are shown. The direction is often across or against the wind.

180. Grant, K. J. (1937). "Some recent migrations of the silver Y moth." S. East Nat. 42: 99–106.

A short discussion on the types of British migrant Lepidoptera. A short summary of records made, from 1932 to 1936, of the migrations of *Plusia gamma*, the silver-Y moth. The effects of wind. In about sixty records of migratory flights there is a slight preponderance of flights against the wind over flights with it. The improbability of *Plusia gamma* surviving the winter in England.

181. Goodall, C. J. (1938). "*Euphrydryas aurinea* in Herts." Entomologist, 71: 162.

A further instance of a single specimen of this local butterfly being found at a considerable distance from the nearest known colony.

182. Morley, A. M. (1938). "*Aplasta ononaria* at Folkestone." Entomologist, 71: 145–7.

Eight specimens, probably all descendants of a single female immigrant moth, were taken. All previous records of its occurrence in this country are listed. Further reference in **E. A. Cockayne** (1938). Entomologist, 71: 169–73.

183. Shrubsole, G. (1937). "Mollusca of the sheep ponds on the Eastbourne Downs." J. Conch. 20: 308–10.

A discussion on the method of colonization of artificial ponds near Eastbourne by Molluscs. The author attributes their presence to human agency.

8. REPORTS OF ORGANIZATIONS

184. Committee on Bird Sanctuaries in Royal Parks (England) (1938). "Report for 1937." (London: H.M. Stationery Office. Price 6*d*.)

Contains chiefly records, but some interesting, though scrappy, data on fluctuations of winter gull and water fowl populations.

185. Fisheries—England and Wales. Minist. Agric. Fish. (1937). "Salmon and freshwater fisheries: Report for the year 1936." Pp. 1–53. (London: H.M. Stationery Office. Price 1*s*.)

A graph shows annual fluctuations since 1909 in catch of salmon and migratory trout from 14 districts. There is a general similarity of trend. Abundant rainfall and an increase in efficiency of sewage disposal reduced the effects of pollution. Research was carried out on pollution by cyanide and tar acids in the Tyne, lead in a Welsh river, road dressings and milk wastes; on biological indicators of pollution; on the growth of brown trout and their eggs in soft waters.

186. Anon. [1937]. "Saorstát Éireann [Irish Free State] Report on the sea and inland fisheries for the year 1936." Pp. 1–32. (Government Publications Sale Office, 5 Nassau St., Dublin, C. 2. Price 9*d*.)

Eighteen appendices with short discussion. The Department examined samples of herring (young herring have become very scarce off the Donegal coast), carried out a salmon marking scheme and a study of the food and growth of brown trout in acid and alkaline waters.

187. Éire, Dep. Agric., Fish. Branch [1938]. "Report on the sea and inland fisheries for the year 1937." Pp. 1–35. (Government Publications Sale Office, 3–4 College St., Dublin. Price 9*d*.)

Statistics of catches and prices of marine and inland fisheries. Sea fisheries include demersal fishes (not separated into species), herring and mackerel and shellfish. Inland fisheries include salmon, trout and eels. Brief non-technical accounts of investigations into the biology of the herring, plankton and hydrography, salmon and trout are given with a summary of legislative measures.

188. Dove Marine Laboratory, Cullercoats, Northumberland (1938). Report for the year ending 31 July 1937. Third series, No. 5, 42 pp. (Marine Laboratory Committee of King's College, Newcastle upon Tyne. Price 5*s*.)

Includes a report of herring investigations and notes on fish living and breeding in the aquarium. A separate paper on conditioned responses in fishes is noticed elsewhere. (No. **70**.)

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING AT UNIVERSITY COLLEGE, LONDON

5—6 JANUARY 1939

Soirée in the Department of Botany

ON the evening of Friday, 5 January, about 80 members and guests were entertained at a soirée in the Department of Botany, University College, London.

An interesting series of exhibits was shown. Dr F. W. Jane showed a large number of very beautiful drawings and microscopic preparations of a large number of little known British flagellates. Many species of flagellates appear to be rare because not looked for at all, or at the wrong time of the year. Included in the exhibit were many hitherto undescribed species and even genera. A rough classification of habitats was suggested, and the habitat was shown for each of the species. Other exhibits showed the appearance of "annual rings" in sections of the fossil *Lyginopteris*, and vivipary in the fruiting heads of *Dipsacus vulgaris*.

Prof. Salisbury exhibited a series of full-scale drawings of the root systems of dune plants excavated by blowing away of sand. They included *Calluna vulgaris*, *Lotus corniculatus* (80 cm.), *Euphorbia portlandica*, *E. paralias* (130 cm.), *Hypochaeris radicata* (60 cm.) and *H. glabra* (60 cm.), *Ononis arvensis* (150 cm.), *Galium verum* (150 cm.), *Diplotaxis tenuifolia* (70 cm.), *Salvia verbenaca* and *Eryngium maritimum* (155 cm.).

At 9 p.m., Sir Arthur Hill gave an interesting talk on "The Art of living upside-down". He described the reaction of flowers to suspension in inverted positions, and illustrated the resultant types of movement by a large series of specimens, photographs and drawings. He pointed out also the interest of the natural inversion of leaves of *Alstroemeria* and *Bomarea* and of the positions taken up by the pitchers of Nepenthes.

The Annual Meeting

The twenty-fifth annual meeting of the Society was held in the Department of Botany, University College, London, on the following morning, Friday, 6 January, at 10 a.m., the President, Prof. A. G. Tansley, occupying the chair.

Prof. Tansley explained how pressure of work had made him unable to prepare a presidential address, and how the Council had made arrangements for it to be read at a meeting at Easter.

The minutes of the previous meeting were read and confirmed. The resignation of Mrs Hands was accepted and Mr Elflyn Hughes was elected to the membership of the Society. The report of the Hon. Secretary was then read and adopted.

Hon. Secretary's Report for the year 1938

The twenty-fourth annual meeting of the Society was held in the Botany School, Cambridge, on 6 January. On the evening of Friday, 5 January, between 80 and 100 members and guests were entertained at a soirée in the department where a large series of exhibits had been set out.

The Annual Meeting was held on the 6th, and after the business meeting seven very interesting papers were read to the Society. On the following morning a party of 30 under the leadership of Dr Godwin and Mr Tidmarsh, made an excursion by bus through the south-eastern fens and the Breckland margin. The sincere thanks of the Society are due to Prof. Brooks for having given us the generous hospitality of his department.

A new departure in the arrangements of the Society was the holding of an additional

meeting on 20 April in the Botany Department of Bedford College, London, to discuss problems of soil toxicity in Dorset heathland. After introductory accounts by Prof. Neilson-Jones and Dr Rayner, a long and interesting discussion followed, in which several distinguished guests spoke of the problems in relation to their own fields of forestry and soil science. After lunch there followed the inspection of a long series of exhibits illustrating different aspects of the problem. We are greatly indebted to Prof. and Mrs Neilson Jones and their assistants for an extremely profitable meeting.

The Summer Meeting of the Society was held in the University College of Wales, Aberystwyth, from 16 to 21 July. Several expeditions of very great interest were made to Tregaron Bog, to the Dovey dunes and salt marshes, to the Welsh Plant Breeding Station and to the field experiments in the Welsh mountains. A soirée was held on the evening of 16 July and evening meetings were held on the 19th and 20th. About 30 members attended the meeting and a number of these remained after the 21st and were conducted on further local ecological excursions. The Society has seldom had so successful a Summer Meeting and must be extremely grateful to Profs. Newton, Laurie and Stapledon, and their staffs for contributing so wholeheartedly and successfully to it.

In the past year two numbers of volume seven of the *Journal of Animal Ecology* have been published, appearing respectively in May and November; they contain respectively 198 and 226 pages. Twenty-eight original papers were published with 14 plates, in addition to notices and reviews. Notices of publications on Animal Ecology in this volume totalled 288.

Since the last annual meeting there have been issued two numbers of the *Journal of Ecology*, appearing in February and August, and containing respectively 254 and 247 pages with 7 plates. In this volume have been published 26 original papers, as well as notes and book reviews.

The Society's transplant experiments at Potterne are continuing satisfactorily in the hands of Mr Marsden Jones and Dr Turrill, and accounts of them occur in the current issue of the *Journal of Ecology*.

Since the last annual meeting the membership of the Society has risen from 350 to 363 members. 12 members have resigned or have died, and 25 new members have been elected. Of the present membership list 193 members received the *Journal of Ecology* alone, 116 the *Journal of Animal Ecology* alone, 52 received both *Journals* and one neither.

During the year the Society has suffered the loss by death of several valuable members, among them Mr B. D. Burtt and Mr C. F. M. Swynnerton, killed during air reconnaissance in East Africa, Prof. A. E. Boycott, F.R.S., and Prof. J. W. Bews, both men of the highest rank in our science. Prof. Boycott had been president of the Society in 1932 and 1933.

We are glad to note in the New Year's Honour's List the name of Sir R. G. Stapledon, an ecologist in practice and agriculturist in profession.

This year marks the end of the very long and devoted service of Mr Boyd Watt as Hon. Treasurer to the Society. We offer him our deep thanks for his able handling of our affairs and give him our sincerest good wishes.

The Hon. Treasurer made a provisional statement on the financial position of the Society, reporting a considerable positive balance on the year's working (see statement on p. 249). It was proposed from the chair and accepted *nem. con.* that Messrs William Norman and Son be reappointed auditors of the Society for 1939. Similar approval was given for grants of £5 to the Society's transplant experiments and of £10 to the Freshwater Biological Association.

The President then explained to the meeting that in view of Mr Boyd Watt's twenty-five years devoted service to the Society, the Council had nominated him on retirement from his post as Hon. Treasurer for Hon. Life Membership of the Society. This was carried with acclamation.

The alterations of rules proposed by the Council, to give effect to their wish that there should be two Hon. Treasurers and two Hon. Secretaries, were explained by the President and Hon. Secretary and were agreed *nem. con.* (for rules so approved see p. 251).

The meeting then proceeded to the election of officers and council members as follows:

Vice-President: Mr C. Diver (Dr Turrill retiring).
Hon. Treasurers: Dr A. S. Watt and Mr V. S. Summerhayes.
Hon. Secretaries: Dr H. Godwin and Dr G. C. Varley.
Ordinary Council Member: Dr O. W. Richards (Dr Ashby retiring).

The President then mentioned the arrangements for the Easter Meeting, which by the kindness of Prof. William Brown would be held in Imperial College, South Kensington. He mentioned the possible alternatives of the New Forest or Plymouth for the Summer Meeting, and outlined a scheme for a National Atlas, in the preparation of which the Society had been asked to co-operate. The Hon. Secretary briefly indicated the steps which the Council had taken to co-operate with the Forestry Commission in initiating a scheme for Ecological reserves in different parts of the country.

Mr Richard Freeman, Magdalen College, Oxford, was elected a member of the Society.

The President read a letter from Mr Dudley Stamp suggesting the possibility of having a mechanism for life membership of the Society instead of the payment of annual subscriptions: it was agreed to refer the matter to the Council.

At 11.10 a.m., the President opened the symposium on the Reciprocal Relationship of Ecology and Taxonomy. An account of the proceedings will be found in the *Journal of Ecology*. Those who spoke were:

The President
Prof. E. J. Salisbury
Dr O. W. Richards
Dr J. Huxley, F.R.S.
Dr D. H. Valentine
Capt. C. Diver
Mr V. S. Summerhayes
Dr J. Burtt Davy
Mr A. J. Wilmott
Dr B. P. Uvarov
Dr A. R. Clapham
Mr C. B. Williams
Mr C. S. Elton
Mr R. Ross
Mr H. Baker
Dr H. Godwin
Dr A. S. Watt
Mr F. T. K. Pentelow
Dr W. B. Turrill

The discussion continued through the afternoon. In adjourning the meeting the President gave very hearty thanks to Profs. Salisbury and Hill for their hospitality, and to Prof. Salisbury and Dr Barbara Russell-Wells for the trouble they had taken in organizing the soirée and the meeting. The meeting closed at 4 p.m. with tea generously provided by Prof. Salisbury.

EASTER MEETING, 1938

A special meeting of the Society was held in the Botany Department, Bedford College, London, at 11 a.m., on 20 April 1938, the President, Prof. A. G. Tansley, in the chair. Several distinguished guests were present by invitation, Dr Crowther, Dr Jacks, Dr Lewis, Dr Guillebaud and Sir Albert Howard.

An informal account was given by Prof. Neilson Jones of some of the characteristics, including that of apparent toxicity, associated with the soils of Wareham Heath. He described the poor growth of conifers in this soil and showed that *Nicotania* seedlings grown in pots of it only thrive at the margins. He showed that steaming the soil mitigated the effect, and that the vapour from steamed soils produced epinastic movements in tomato like those produced by ethylene. In a film of nutrient agar poured over the soil, fungal spores germinate but the hyphae do not grow: steaming and other pre-treatments remove this effect. The condition of "fused needle" in *Pinus contorta* and *P. insignis* was described and it was said that no pathogen had been detected.

This was followed by a general description, given by Dr M. C. Rayner, of research work done at Wareham since 1932, with special reference to forestry experiments. She showed that seedlings on the sterile soil had no tertiary roots and no mycorrhiza, and demonstrated that good growth and good mycelium go together. The beneficial effects of the addition of composts of straw, hops, sawdust and *Molinia* to the soils were described, and illustrated by very striking photographs.

An extremely interesting and controversial discussion followed, in which many members and guests took part.

After lunch the meeting examined a long series of exhibits dealing with the same problems, and discussed the exhibits with the individual research workers who had produced them.

The discussion was resumed at 3.30 p.m., and some time later closed with a very delightful tea party given in the College. Prof. Tansley expressed the grateful thanks of the Society for the generous hospitality given us by Prof. and Mrs Neilson Jones, their research workers, and the College authorities.

SUMMER MEETING AT ABERYSTWYTH

16—21 July 1938

At the kind invitation of Profs. Newton, Laurie and Stapledon, the Summer Meeting of the Society was held at Aberystwyth. The meeting opened with a soirée held in the University College of Wales, at 8.15 p.m. A large number of interesting exhibits had been set out, and during the evening songs were given by some of the University students.

Sunday, 17 *July*. A visit was paid to Tregaron Bog under the leadership of Dr Godwin. The large west bog is a typical atlantic raised-bog (Hochmoor) with a well developed rand beside the river Teifi, and remains of a lagg where the bog meets the hillside. The highest part of the bog is occupied by very characteristic regeneration complex in which pools and *Sphagnum* hummocks alternate.

Monday, 18 *July*. The meeting visited the gardens of the Welsh Plant Breeding Station, where Dr Jenkin demonstrated the basis of production of seed for pasturing. He emphasized the need for selection for permanence, leafiness and vigour. He stressed the extremely heterozygous nature of the material and its great phenotypic variation. In the greenhouse Dr Jenkin described the genetical work on *Lolium* and demonstrated the practical methods of performing crosses. He then showed the party the results of some extremely interesting interspecific and intergeneric crosses, drawing especial attention to the doubtful origin of *Festuca loliacea*. This is supposed to be a cross between *F. pratense* and *Lolium perenne* but indistinguishable plants can be produced in other ways. The party went on to the experiments in the Penglais fields, in which were growing rows of clones of many selected and commercial strains of Timothy and other grasses. The close leafy habit of types selected from old pastures contrasted strongly with the stemmy open growth of the commercial strains. The testing for late flowering and resistance to rust were also demonstrated.

Following an improvement in the weather the party travelled in the afternoon to visit the Cahn Hill Improvement Scheme. All the hill-pasture experiments were concerned more or less with the influence of the biotic factor on sward development. Many remarkable effects were shown of treatment by phosphates or basic slag, with or without the introduction of new species such as wild white clover and Yorkshire fog. There was a very marked effect of the transport of minerals with "stock nitrogen" from the lower manured slopes to higher pastures. In particular the effects of night camping by cattle in sheltered hollows at high altitudes, was very strongly marked, such areas showing a great increase in *Agrostis* and establishment of clover.

In the evening at 8 p.m., there was a small exhibit staged in the Botany Department of University College, of various aspects of the work of the Plant Breeding Station, and different members of the staff gave short talks on genetical and ecological aspects of their

work. Dr Jenkin gave an account of genetics in relation to ecology, drawing examples from his very wide experience of the grasses. A point of particular interest was the occurrence of two types of *Arrhenatherum elatius*. The extreme bulbous type is found in arable land, and most hedgerow or wayside plants are intermediate in type. Completely non-bulbous plants have to remain winter green. The *F*1 crosses between the extreme types are intermediate. Mr R. D. Williams described his work on genotypes of red clover. The plants are diploid (2×7) and normally cross-fertilized with very common self-sterility. He showed specimens illustrating the determinance of several features such as pubescence, dwarfness, sterility and chlorophyll-deficiency. Marked linkage groups have been demonstrated. Mr W. Davies gave a short description of the grasslands of Wales, and stressed the fact that altitude and geology are not the only factors determining grassland type. He suggested that the dominance of *Agrostis* is largely due to grazing. Prof. Stapledon concluded the series by some general remarks on the ecology of Welsh pastures, again pointing out the great importance of grazing treatment.

Tuesday, 19 *July*. The party visited Llety-evan-hen to see the experiments of the Welsh Plant Breeding Station on controlled grazing and manuring upon native *Molinia* and *Fescue-Agrostis* swards. The cages under different manurial treatment and strictly controlled grazing showed extremely marked differences from one another, although only begun in 1930. It was very marked that new species made their appearance wherever suitable conditions were created, although no seeds were sown, and although samples showed no buried viable seeds. Within two years the controlled grazing and manuring changed the former *Molinia-Nardus* sward to *Fescue-Agrostis*. After lunch at the Plant Breeding Station the party was shown experiments on grazing and manuring in a valley marsh, where changes as striking as those on the upland pastures were evident. Across one set of plots there was an extremely marked low-fertility strip on the site of a former hedgerow.

At 8 p.m. in the Department, the following series of short papers were given:

"Distribution of hill bogs in Cardiganshire": J. B. Jones.
"Soil Fauna of the Dovey Estuary": Dr Watkin.
"Preliminary account of Blaen Brefi bog (1300 ft.)": E. G. Davies.
"Observations on *Rhynchospora alba*": E. M. Canton.
"Tregaron Bog": H. Godwin.

Wednesday, 20 *July*. The party visited the sand dunes at Ynyslas under the leadership of Mr E. H. Chater. The dunes showed very marked effects of wind erosion and rearrangement, and extensive dune lows and sandy marshes. The effect of blowing sand in promoting the flowering of *Psamma* was very well seen. After lunch the party visited the salt marshes on the shores of the Dovey Estuary, and were shown the evolution of different types of pans from channels and depressions to their final disappearance into close sward. It was quite clear that several different levels of marsh were represented, and distinct phases of erosion and deposition following changes in the course of the Dovey currents.

In the evening there was an exhibition in the Department of Zoology of work on Animal Ecology and the following papers were read:

"Faunistic history of River Rheidol in relation to lead pollution": Dr K. E. Carpenter.
"Remarks on effect of pollution on plants": Prof. Newton.
"The effect of calcium on the toxicity of heavy metal salts to fish": Dr J. R. E. Jones.

At the conclusion of the meeting Prof. Tansley expressed our deep gratitude to our hosts for providing such an exceptionally interesting and satisfactory meeting. He expressed particular thanks to Profs. Newton, Laurie, and Stapledon and the stewards, Mr J. B. Jones and Mr E. G. Davies who had so successfully organized the excursions.

Several members prolonged their stay beyond the official end of the meeting, and were taken on further ecological excursions into the woodland and mountain pastures of the district.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1938

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance		475 18 0
Interest on Investments	39 15 0	
Interest on Deposit Account	1 5 0	
		41 0 0
Index volume to *Journal of Ecology*, vols. I–XX:		
Sales	15 18 0	
Expenses	3 7 4	
		12 10 8
		£529 8 8
Journal of Ecology, 1938:		
Sales: Current vol. XXVI, 1938		559 0 0
Back volumes and parts		41 6 8
Reprints of papers		67 2 0
Grant: Received per Editor		10 0 0
		677 8 8
Balance (see above, under Expenditure)		45 11 2
		£722 19 10
Journal of Animal Ecology, 1938:		
Sales: Current vol. VII, 1938		250 18 8
Back volumes and parts		95 5 2
Reprints of papers		54 17 0
		401 0 10
Grant: From Bureau of Animal Population, Oxford		5 0 0
		406 0 10
Balance (see above, under Expenditure)		236 0 10
		£642 1 8

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing, Stationery, etc.	5 5 6	
Postages and Travelling	13 13 5	
Bank Charges	1 3 3	
Clerical assistance	15 0 0	
Meetings, Soirée, etc.	2 4 0	
Audit	3 3 0	
		40 9 2
Grants:		
Fresh Water Biological Association	10 0 0	
Transplants Experiments Fund	5 0 0	
		15 0 0
Journal of Ecology. Cost *less* Sales		45 11 2
Journal of Animal Ecology. Cost *less* Sales		236 0 10
		337 1 2
Balance: Surplus for the Year, carried forward		192 7 6
		£529 8 8
Journal of Ecology, 1938:		
Cost: Paper, Blocks, Printing and Binding		599 4 7
Publishers and Commission		84 9 8
Carriage and Postages		35 5 7
Insurances		4 0 0
		£722 19 10
Journal of Animal Ecology, 1938:		
Cost: Paper, Blocks, Printing and Binding		550 19 10
Publishers' Commission		51 2 5
Carriage and Postages		20 13 11
Insurance		6 16 3
Sundries		2 9 3
Bureau of Animal Population, Oxford, for special services		10 0 0
		£642 1 8

BALANCE SHEET AT 31 DECEMBER 1938

Liabilities

	£ s. d.	£ s. d.
Subscriptions prepaid for 1939/31		18 9 0
Library Fund		1 5 0
General Revenue Account, Surplus in hand:		
Balance at 31 December 1937	1087 11 3	
Surplus for the Year 1938	192 7 6	
		1279 18 9
		£1299 12 9

Assets

	£ s. d.	£ s. d.
Cash in Hand at Westminster Bank:		
Current Account	27 11 11	
On Deposit	200 0 0	
		227 11 11
Investments at Cost:		
Brought forward, 31 December 1937	915 13 0	
Bought February 1938, £150 of 3½ % War Loan ...	156 7 10	
		1072 0 10
		£1299 12 9

Totals held, 31 December 1938:	£ s. d.
£850 of 3½ % War Loan at cost ...	873 10 10
£200 of 5 % Conversion Loan ...	198 10 0
	£1072 0 10

NOTE A. The market value of the above Investments at 31 December 1938:

3½ % War Loan at 98	£833
5 % Conversion Loan 109½	£219
	£1052

NOTE B. A further Asset not valued above is the unsold Stock of Journals and Index Volumes held by the Publishers for the Society.

(Signed) HUGH BOYD WATT,
Hon. Treasurer.

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates, and also the Investments.

(Signed) WM NORMAN & SONS.
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.

1 *February* 1939

THE BRITISH ECOLOGICAL SOCIETY

FOUNDED 1913

CONSTITUTION AND RULES

1. The object of the BRITISH ECOLOGICAL SOCIETY shall be to promote and foster the study of Ecology in its widest sense.

2. The Society shall consist of Ordinary Members, Hon. Members and Associates as defined in these rules.

3. Applicants for Membership of the Society shall be proposed by one Member (from personal knowledge) or by an Officer of the Society (not necessarily with personal knowledge) and seconded by one or more other Members. Such applications shall be made on a form to be supplied by the Hon. Secretaries, and duly filled up and signed by the applicant.

Election shall take place either at a General Meeting or at other times by resolution of the Council. A majority of votes in favour shall result in the election of the applicant.

The Secretaries may, however, be empowered by the Council to circulate the names of applicants for membership to members of Council by post, and if they receive no intimation of objection within one week, the applicant shall be deemed to be elected.

4. Subscriptions shall be payable in advance and shall be due on January 1st each year. The minimum Annual Subscription for Ordinary Membership shall be twenty-five shillings (25*s.*) and for Associate Membership seven shillings and sixpence (7*s.* 6*d.*). Members who pay a yearly subscription of 25*s.* shall have the right to receive post free **either** *The Journal of Ecology* **or** *The Journal of Animal Ecology*. An Annual Subscription of 45*s.* shall entitle Members to receive post free **both** of the Journals above named.

5. In addition to receiving one or both of the Journals of the Society, ordinary members shall have the following privileges:

(*a*) To receive on application any other publications of the Society free or at a reduced rate, as the Council may from time to time determine.

(*b*) To have the use on loan, under regulations, of any photographs or lantern slides in the Society's collections, and of books, maps and pamphlets in the Society's Library.

(*c*) To vote in the election of Council and of Officers.

(*d*) To be eligible for service on the Council and its Committees, or as Officers.

6. Associate Members shall have the right to attend Meetings and Excursions, to obtain through the Secretaries such advice and assistance as the Society can afford, to have the use of photographs and the Library, but they shall not have the privileges of Ordinary Members indicated in 5 (*c*) and 5 (*d*).

7. Local Natural History Societies may at the discretion of the Council be allowed to subscribe to the Society not less than twenty-five shillings (25*s.*) per annum and shall thereby be entitled to receive a copy of **either** of the two Journals of the Society, or on payment of forty-five shillings (45*s.*) per annum, to receive **both** Journals of the Society. In either case they shall also be entitled (*a*) to such advice or assistance as the Society can afford, and (*b*) to send two delegates to the Society's Meetings, to have the same privileges as Associate Members as regards such Meetings.

8. The Society shall be governed by a Council of not less than fifteen, and not more than twenty Members consisting of the Officers of the Society, namely, the President, two Vice-Presidents, the two Hon. Editors, the two Hon. Secretaries and the two Hon. Treasurers, with ordinary members of Council.

Officers and ordinary members of Council shall be elected at the Annual Meeting of the Society.

9. Each ordinary member of Council shall be elected for a period of four years, at the end of which time he shall retire. He shall not be eligible for re-election until the Annual Meeting of the year following that of his retirement.

An ordinary member of Council when elected an Officer of the Society shall cease to be an ordinary Council member: on expiry of office the retiring President, Hon. Secretaries, Hon. Treasurers and Hon. Editors shall be eligible for immediate re-election as ordinary members of Council, and the retiring Vice-President shall complete his term of four years' service on the Council.

10. The President and the two Vice-Presidents shall be nominated from among the members of Council. The two Hon. Editors and the two Hon. Secretaries shall retire at the end of each year but shall be eligible for immediate re-election.

11. The President of the Society shall hold office for two years, and it shall be his duty to deliver an address to the Society at the Annual Meeting next after that at which he was elected.

12. One Vice-President shall be appointed each year and shall hold office for two years.

13. The two Hon. Treasurers shall hold office for three years and shall be eligible for re-election. The Hon. Treasurers shall keep the Society's funds and shall be responsible for collection of subscriptions. Their sanction shall be required for the disbursement of the Society's moneys and they shall present a financial statement at the Annual Meeting. The financial status and policy of the Society shall be considered each year at a meeting of the Council held as soon as practicable after the audit. The audited accounts shall be published in the Journals of the Society.

14. If any Council member does not attend at least one meeting of the Council during the year he shall retire at the end of the year, but shall be eligible for re-election.

15. At least one fortnight before the Annual Meeting the Secretaries shall circulate to all Members of the Society a list of the members of Council including Officers, indicating those who retire and adding the names of nominees of the Council to fill the vacancies.

16. Members may propose for ballot at the Annual Meeting the name or names of any duly qualified Member or Members in place of any or all of the Council's nominees.

17. The Council shall have power to co-opt any ordinary Member of the Society to fill vacancies occurring during the year among Council or Officers, the tenure of such co-opted Members to terminate at the next Annual Meeting.

18. At the Annual Meeting, after nomination by the Council, persons who have rendered conspicuous service to the subject of Ecology may be elected Honorary Members of the Society.

Such Hon. Members shall receive free either or both Journals of the Society as the Council may determine, and shall also have the other privileges of ordinary Members of the Society.

19. The Annual Meeting shall be held in December or in the following January. At least one other Meeting shall be held later in the year. Further Meetings and Excursions may be held at such times and places as the Council may from time to time determine.

20. At the Annual Meeting the Members of the Society present shall ballot for Officers and Council and consider any other business brought before them by the Council or by any Member, of which four weeks' notice in writing has been given to the Secretaries.

21. Alterations of the Rules shall only be made at the Annual Meeting and require six weeks' notice in writing to the Secretaries and a majority of two-thirds of the Members voting.

22. Members desiring to present communications at any Meeting must give due notice to the Secretaries, stating the nature of the communication and the time required.

23. At any Meeting of the Society the Chairman shall decide as to procedure and the order of business. It shall be within the Chairman's discretion to admit communications or other business, other than alterations to the Rules, not included in the programme.

24. A Meeting of the Council to consider the Annual Report shall be held shortly before the Annual Meeting.

25. The Society shall issue two Journals, *The Journal of Ecology*, and *The Journal of Animal Ecology*.

26. The subscription price of each Journal to others than Members of the Society shall be as determined by the Council.

27. No Member shall be entitled to receive the Journals of the Society whilst his subscription is in arrear.

(This revised formulation of the constitution and rules was accepted at the Annual Meeting of the Society, 6 January 1939.)

LIST OF MEMBERS (16 JANUARY 1939)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
A. **Alexander**, W. B., M.A.; University Museum, Oxford.
A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
A. **Allen**, E. F., B.A., M.B.O.U.; Dept. of Agriculture, Teluk Anson, Perak, Malaya.
E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dhanna College, Lahore, India.
E. **Andersonian Naturalists' Society** (cf. Glasgow).
E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
E. **Ashby**, Prof. Eric, B.Sc.; The University, Sydney, N.S.W.
E. **Bacon**, Mrs Alice; The Technical College, Brighton.
E. **Baker**, H.; University Dept. of Botany, High St., Oxford.
A. **Barber**, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
E. **Barnes**, Dr B.; 28, Torridon Road, London, S.E. 6.
A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
E. A. **Beauchamp**, R. S. A., B.A.; Connellmore, Cheltenham, Glos.
E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
A. **Bertram**, G. C. L., M.A.; St John's College, Cambridge.
E. **Bhâradwâja**, Prof. Y.; Dept. of Botany, Hindu University, Benares, India.
E. **Bharucha**, Dr F. R.; 6, Alexandra Road, New Gamdevi, Bombay 7.
E. **Blackburn**, K. B., D.Sc.; Armstrong College, Newcastle-upon-Tyne.
E. **Blackman**, G. E.; Wick Cottage, Westleigh Av., Putney Hill, London, S.W. 15.
E. **Bloomer**, H. H.; Longdown, Sunnydale Road, Swanage, Dorset.
E. **Bor**, N. L., M.A., D.Sc.; Forest Research Institute, New Forest P.O., Dehra Dun, U.P. India.
E. **Børgesen**, Dr F. C. E.; Botanisk Museum, Gothersgade 130, Copenhagen.
A. **Bosanquet**, S. J. A.; Fisheries' Laboratory, Lowestoft, Suffolk.
A. **Boyd**, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.
E. **Boyd**, L.; Royal Botanic Gardens, Edinburgh.
E. **Bracher**, Miss Rose, Ph.D.; Dept. of Botany, The University, Bristol.
E. **Braid**, Major K. W.; 6, Blythswood Square, Glasgow.
E. **Braun**, Miss E. L.; 2702, May Street, Cincinnati, Ohio, U.S.A.
E. **Brenchley**, Dr Winifred E.; Rothamsted Experimental Station, Harpenden, Herts.
A. **Brindley**, Mrs M. D.; 25, Madingley Road, Cambridge.
E. **Brodsky**, Prof. A.; Middle Asiatic State University, Tashkent, Usbekistan, U.S.S.R.
E. **Brooks**, Prof. F. T., M.A., F.R.S.; Botany School, Cambridge.
A. **Brown**, F. M.; Bryancliffe, Hungerford Road, Huddersfield, Yorks.
E. **Burges**, N. A.; Botany School, Cambridge.

E. A. **Burtt**, B. L.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Burtt Davy**, Dr J.; Shotover Furze, The Ridings, Headington, Oxford.
E. **Butcher**, R. W., B.Sc.; Fisheries Research Station, Alresford, Hants.
A. **Buxton**, Prof. P. A.; London School of Hygiene, Keppel Street, London, W.C. 1.
E. **de Caen**, Mrs, Ph.D,; Springfield, Dalgany, Co. Wicklow, Ireland.
A. **Cameron**, A. E., D.Sc.; Dept. of Entomology, 10, George Square, Edinburgh.
A. **Carey**, Miss E., Foxhill, Bracknell, Berks.
A. **Carpenter**, Prof. G. D. Hale, M.B.E., D.M.; Penguelle, Hid's Copse Road, Cumnor Hill, Oxford.
A. **Carpenter**, J. R., M.Sc.; 2670, N. Alpine Road, Grand Rapids, Michigan, U.S.A.
A. **Carpenter**, Prof. K. E., Ph.D.; Zoology Dept., University of Liverpool.
A. **Carter**, Dr G. S.; Corpus Christi College, Cambridge.
E. **Carter**, Dr Nellie; Armeria, Petersham Road, Richmond, Surrey.
A. **Cawkell**, E. M., 10, Algier's Road, Ladywell, London, S.E. 13.
E. **Chapman**, P. C.; Charterhouse School, Godalming, Surrey.
A. **Chapman**, Prof. R. N.; University of Hawaii, Honolulu, Hawaii.
E. **Chapman**, V, J.; 13, Brookside, Cambridge.
A. **Charteris**, Hon. Guy; 24, Oxford Square, London, W. 2.
A. **Chitty**, D. H.; Bureau of Animal Population, University Museum, Oxford.
E. **Clapham**, Dr A. R.; Botanical Dept., The University, Oxford.
E. A. **Clements**, Prof. F. E.; Mission Canyon, Santa Barbara, California.
A. **Colquhoun**, M. K.; Lane's End House, Woodlands St Mary, Newbury, Bucks.
E. **Conway**, Miss V. M.; 61, De Freville Avenue, Cambridge.
E. **Cooper**, Prof. W. S.; Dept. of Botany, University of Minnesota, Minneapolis, Minn.
E. **Cotton**, A. D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Corley**, H. V.; Hyron's Lodge, Amersham, Bucks.
E. **Cowles**, Prof. H. C.; University of Chicago, Chicago, Ill., U.S.A. (*Hon. Life Member*).
E. **Croydon Natural History and Scientific Society**, 27, High Street, Croydon.
E. **Curtis**, Miss W. M., B.Sc.; 381, Holly Lodge Mansions, Highgate, London, N. 6.
A. **Dalgety**, C. T.; Denver Hall, Downham Market, Norfolk.
A. **Darling**, F. F., Ph.D.; Brae House, Dundonnell, by Garve, Wester Ross, Scotland.
E. **Davey**, Miss A. J., M.Sc.; University College of N. Wales, Bangor, N. Wales.
E. **Davies**, W. C.; The Cawthron Institute, Nelson, N.Z.
E. A. **Davis**, D. H. S.; Dept. of Public Health, Pretoria, S. Africa.
E. **Davis**, T. A. W.; Forestry Station, Mozaruni, British Guiana.
E. **Dawson**, R. B., M.Sc., F.L.S.; St Ives Research Station, Bingley, Yorks.
E. **Delf**, Dr E. M.; Westfield College, Hampstead, London, N.W. 3.
A. **Diver**, C.; 40, Pembroke Square, Kensington, London, W. 8. (*Vice-President*).
A. **Donaldson**, R. P.; Royal Society for Protection of Birds, 82, Victoria Street, London, S.W. 1.
E. **Dowling**, Miss R. E., M.Sc.; The Nest, Ledgers Road, Slough, Bucks.
A. **Duncan**, A. B., B.A.; Gilchristland, Closeburn, Dumfries.
E. **Dundas**, J.; Chief Conservator of Forests, Ibadan, Nigeria.
E. **Du Rietz**, Prof. Einar; Vaxtbiologiska Institutionen, Upsala, Sweden.
E. A. **Dyke**, F. M., B.Sc.; Branksome, Boreham Woods, Herts.
E. **Edwards**, Miss D. A., 35, Queen's Gate Mews, Kensington, London, S.W. 7.
E. A. **Eggeling**, W. J., B.Sc.; Forest Office, Entebbe, Uganda.
E. **Ekblaw**, Dr W. E.; Clark University, Worcester, Mass., U.S.A.
A. **Ellis**, R.; 2420, Ridge Road, Berkeley, California, U.S.A.
E. A. **Elton**, Charles; Bureau of Animal Population, University Museum, Oxford (*Hon. Editor of the Journal of Animal Ecology*).

E. **Essex Field Club, The** (Essex Museum of Natural History, Romford Road, Stratford, Essex).
E. **Evans**, E. Price; White Broom, 69, Westgate, Hale, Cheshire.
A. **Evans**, F. C.; Oriel College, Oxford.
E. **Evans**, G. C.; Botany School, Cambridge.
A. **Eyre**, Miss J.; Dept. of Zoology, University of Cape Town, S.A.
E. **Falk**, P.; 24, Rokeby House, Rugby.
E. A. **Featherly**, Prof. H. I.; Oklahoma Agricultural and Mechanical College, Stillwater, Okla., U.S.A.
E. **Fenton**, E. Wyllie, D.Sc.; 13, George Square, Edinburgh.
A. **Fidler**, J. H.; Warrenside, Mapledurham, Reading.
E. **Fisher**, H. S., M.Sc.; 35, Alexandra Road, Pietermaritzburg, Natal.
A. **Fisher**, J. M. Mc.; Zoological Society of London, Regent's Park, N.W. 8.
E. A. **Fitzgerald**, D. V.; Clammer Hill, Haslemere, Surrey.
E. **Foggie**, A., B.Sc.; c/o Conservator of Forests, Forestry Department, Accra, Gold Coast, Africa.
A. **Ford**, J.; Tsetse Research Dept., Shinyanga, Tanganyika Territory.
E. **Fraser**, G. K., M.A., D.Sc.; Macaulay Institute, Craigiebuckler, Aberdeen.
A. **Freeman**, R.; Magdalen College, Oxford.
E. **Fritsch**, Prof. F. E., F.R.S.; Pilgrim's End, West Humble, Dorking.
E. **Fuller**, Prof. G. D.; Botany Dept., The University, Chicago, Ill., U.S.A.
E. **Galloway**, J. A.; Oak Bank, Bowness on Windermere, Westmorland.
E. **Gams**, Dr H.; Innsbruck-Hotting, Schreeburggasse 67, Austria.
Garland, R. H. C.; 21 Brading Av., Southsea, Hants. (*Associate member*).
E. A. **Garner**, J. H., B.Sc.; West Riding Rivers Board, 71, Northgate, Wakefield.
E. **Gibson**, Miss C. M.; The Municipal College, Portsmouth.
E. **Gilbert-Carter**, H., M.A., M.B.; Cory Lodge, Botanic Garden, Cambridge.
E. **Gillman**, H., M.Sc.; District Agricultural Office, Bukoba, Tanganyika Territory.
E. **Gilmour**, J. S. L., B.A.; Royal Botanic Gardens, Kew, Surrey.
E. A. **Glasgow and Andersonian Nat. Hist. and Microscopic Soc.**; Societies' Rooms, Royal Technical College, Glasgow.
E. A. **Godwin**, H., Ph.D.; Botany School, Cambridge (*Hon. Secretary*).
E. A. **Good**, R. D'O.; University College, Hull.
E. **Gourlay**, W. B., M.A., M.B.; 7, Millington Road, Cambridge.
E. **Griffith Tedd**, H.; P.O. Box 30, Xanthie, Greece.
E. A. **Griffiths**, B. M., D.Sc.; Dept. of Botany, University Science Labs., South Road, Durham.
A. **Gurney**, Dr R.; Bayworth Corner, Boar's Hill, Oxford.
E. **Halket**, Miss A. C., B.Sc.; Bedford College, Regent's Park, London, N.W. 1.
E. **Halliday**, W. E. B.; c/o Dominion Forest Service, 813, New Federal Building, Winnipeg, Manitoba, Canada.
E. A. **Hancock**, G. L. R.; Makenene College, Box 262, Kampala, Uganda.
E. **Hanson**, Dr Herbert C.; Botanist and Head of Dept. of Botany, North Dakota Agric. College and Expt. Station, Fargo, North Dakota, U.S.A.
A. **Hardy**, Prof. A. C., M.A.; University College, Hull (*Vice-President*).
E. **Hare**, C. Leighton, B.Sc.; Department of Botany, The University, Aberdeen.
A. **Hare**, Prof. T., M.D.; 70, Holywell Hill, St Albans.
E. **Harley**, J. H.; University Dept. of Botany, High Street, Oxford.
E. **Harris**, C. M.; Forest Office, Entebbe, Uganda.
A. **Harris**, W. V.; Dept. of Agriculture, Morogoro, Tanganyika Territory.
E. **Harrison**, A. B.; The Hollies, Farndon, Newark-on-Trent.
A. **Hartley**, C. H., B.A.; Eton College, Windsor, Bucks.

A. **Harvey**, A. L., M.Sc.; Dept. of Zoology, University College of S.W. England, Exeter, Devon.

E. **Heddle**, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric., 13, George Square, Edinburgh.

E. A. **Heslop Harrison**, Prof. J. W.; Dept. of Botany, King's College, Newcastle-upon-Tyne.

E. **Hewetson**, C. E.; Indian Forestry Service, Jubbulpur, Central Provinces, India.

E. **Hilary**, Miss D., B.Sc.; 15, Plevna Terrace, Bingley, Yorks.

E. **Hill**, Sir A. W., F.R.S.; Royal Botanic Gardens, Kew, Surrey.

E. **Hill**, Prof. T. G.; University College, London, W.C. 1.

A. **Hobby**, B. M., M.A., D.Phil.; University Museum, Oxford.

A. **Hodgkin**, E. P.; Institute for Medical Research, Kuala Lumpur, F.M.S.

E. **Holch**, Dr A. E.; Botany Dept., University of Denver, Colorado, U.S.A.

E. **Hole**, D. R., B.Sc.; Rousdon, Cutbush Lane, Shinfield, Reading.

E. **Holttum**, R. E., M.A.; The Botanic Gardens, Singapore.

E. **Hope Simpson**, J. F.; University Dept. of Botany, Oxford.

E. **Horne**, F. R.; Seale-Hayne Agric. College, Newton Abbot, Devon.

E. **Howarth**, W. O.; Botany Dept., The University, Manchester.

E. **Hubbard**, C. E.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.

E. **Hughes**, R. E.; School of Agriculture, University College, Bangor.

E. **Hugh-Jones**, P.; King's College, Cambridge.

A. **Hume**, Capt. C. W.; 284 Regent's Park Road, Finchley, London, N. 3.

A. **Huntingdon**, E.; Dept. Geological Sciences, 4, Hillhouse Avenue, New Haven, Connecticut, U.S.A.

E. **Hutchinson**, R. R.; 11, Fryston Avenue, Croydon.

E. **Hyde**, H. A., M.A.; National Museum of Wales, Cardiff, S. Wales.

A. **Imms**, D. A., D.Sc.; Zoological Dept., Cambridge.

E. **Ingold**, C. T., Ph.D., University College, Leicester.

E. A. **Jackson**, C. H. N., Ph.D.; Dept. of Tsetse Research, Shinyanga, Tanganyika Terr.

A. **Jary**, S. G.; South-Eastern Agricultural College, Wye, Ashford, Kent.

E. **Jennings**, A. E.; Carnegie Museum, Pittsburg, Pa., U.S.A.

E. **Jones**, E. W.; Imperial Institute of Forestry, Oxford.

E. **Jones**, Miss G. M.; The Cottage, Wraysbury, Bucks.

E. **Kashkarov**, Prof. D.; Wasiliewsky Isle, University's Quaie 7/913, University, Leningrad, U.S.S.R.

E. **Kawada**, Prof.; Forest Experiment Station, Shimomeguro Meguro, nr Tokio, Japan.

A. **Kay**, G. T.; 51 St Olaf Street, Lerwick, Shetland Is.

E. A. **Kendeigh**, S. C., Ph.D.; Experimental Zoology Laboratory, University of Illinois, Wright and Healey Streets, Champaign, Illinois.

E. **Killian**, Prof. A.; Faculté des Sciences, L'Université d'Alger, Algeria.

A. **Kitching**, J. A., B.A.; Birkbeck College, Fetter Lane, London, E.C. 4.

E. **Knight**, Miss E. M.; The Lister Institute, Chelsea Bridge Road, London, S.W. 1.

A. **Lack**, D.; The School, Dartington Hall, Totnes.

E. **Landon**, F. H.; c/o Forest Dept., Kuala Lumpur, F.M.S.

A. **Latter**, O. H.; The Elms, Charterhouse Road, Godalming, Surrey.

E. **Laughton**, F. S.; Assistant Forest Officer, Concordia, Knysna, C.P., S. Africa.

E. **Leach**, Prof. W.; Dept. of Botany, University of Manitoba, Winnipeg, Canada.

A. **Lemare**, D. W.; Fisheries Dept., Singapore, Straits Settlements.

A. **Lemon**, F. E.; Royal Society for Protection of Birds, 82, Victoria Street, London, S.W. 1.

E. A. **Lewis**, A. H.; Upcott, Wellington College, Berks.

A. **Lewis**, D. J., M.A.; Agricultural Research Service, Wad Medani, Sudan.

E. **Lewis**, Prof. F. J.; University of Alberta, Edmonton, Alberta, Canada.
E. **Lind**, Miss E. M., B.Sc., Ph.D.; The University, Sheffield.
A. **London Natural History Society**; c/o L. Parmenter, 94, Fairlands Avenue, Thornton Heath, Surrey.
A. **Lotka**, Dr A. J.; Metropolitan Life Insurance Co., 1 Madison Avenue, New York, U.S.A.
E. **Lüdi**, Dr W.; Mohrlistrasse 93, Zurich, Switzerland.
A. **Macan**, T. T.; Wray Castle, Ambleside, Westmorland.
A. **MacLagan**, D. S., D.Sc., Ph.D., F.R.E.S.; King's College, University of Durham.
A. **MacLeod**, J., Ph.D.; The Cooper Field Research Station, Little Gaddesden, Berkhamsted, Herts.
E. A. **MacLulich**, D. A.; Algonquin Park, P.O., Ontario, Canada.
E. **McLean**, Prof. R. C.; University College, Cardiff, S. Wales.
E. **McLuckie**, J., D.Sc.; Dept. of Botany, The University, Sydney, N.S.W.
E. **Mangham**, Prof. S., M.A.; University College, Southampton.
A. **Marples**, Prof. B. J.; Dept. of Biology, Otago University College, Dunedin, New Zealand.
E. **Marquand**, C. V. B., M.A.; Langdale, 56, Broadhurst, Ashstead, Surrey.
E. **Marsden-Jones**, E. M.; The Potterne Biological Station, nr Devizes, Wilts.
E. **Martin**, J. D.; Assistant Conservator of Forests, Lusaka, District Forest Office, Bombwe Forest, Livingstone, N. Rhodesia.
E. **Mason**, E. W.; Inglenook, 63, King's Road, Richmond, Surrey.
A. **Matheson**, C.; Dept. of Zoology, National Museum of Wales, Cardiff.
E. **Matthews**, Prof. J. R., M.A.; The University, Old Aberdeen.
A. **Mellanby**, K.; The University, Sheffield.
A. **Meynele**, M.; Hoar Cross, Burton-on-Trent, Staffs.
E. A. **Michelmore**, A. P. G., B.A.; Saffron Close, Chudleigh, S. Devon.
A. **Middleton**, A. D.; Jealott's Hill Agricultural Research Station, Warfield, Berks.
E. A. **Middleton**, A. R.; Biological Labs., University of Louisville, Louisville, Kentucky, U.S.A.
Miller, W. B.; Sojourner's Club, Fort Bayard, New Mexico, U.S.A.
E. A. **Milne-Redhead**, E., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Mitchell**, M. V.; Grayrigg, Old Colwyn, N. Wales.
E. **Misra**, Dr. R. D.; Botanical Dept., Hindu University, Benares, India.
E. **Mohan**, N. P., M.A.; c/o Lloyds Bank, The Mall, Lahore, Punjab, India.
A. **Mohr**, C. O.; State Natural History Survey, Urbana, Illinois, U.S.A.
A. **Montford**, H. M., B.Sc.; Armeria, Petersham Road, Richmond, Surrey.
A. **Moon**, H. P., B.A.; Dept. of Zoology, University College, Southampton.
E. **Mooney**, H. F., M.A.; Sambalpur, Orissa, India.
E. A. **Moore**, Barrington; Stone Acre, Corfe, Taunton.
E. **Moore**, E. J.; Central Technical College, Birmingham.
E. **Murray**, J. M., B.Sc.; 76, Hillview Terrace, Corstorphine, Edinburgh, 12.
A. **Nelmes**, E. M.; 27, Westbourne Avenue, Acton, London, W. 3.
E. A. **Newman**, Leslie F., M.A.; St Catharine's College, Cambridge.
E. A. **Newton**, Prof. Lily, M.Sc., Ph.D.; Dept. of Botany, University College of Wales, Aberystwyth, Wales.
E. **Nichols**, Prof. G. E.; Botany Dept., Yale University, New Haven, Conn., U.S.A.
A. **Nichols**, J. E., Ph.D.; Dept. of Agric., University of W. Australia, Crawley.
A. **Nicholson**, E. M.; 13 Upper Cheyne Row, London, S.W. 3.
E. A. **Nurse**, H. P.; 120, Culverhay, Ashstead, Surrey.
E. **Ogg**, W. G., M.A., Ph.D.; Macaulay Inst. for Soil Research, Craigiebuckler, Aberdeen.
E. A. **Oldham**, Charles; Oxfield, Berkhamsted, Herts.

E. **Oliver**, Prof. F. W., F.R.S.; Burg-el-Arab, Mariut, Egypt.
E. A. **Oliver**, W. R. B., D.Sc.; Dominion Museum, Wellington, N.Z.
E. **Olmsted**, C. E.; Dept. of Botany, University of Chicago, U.S.A.
A. **Omer-Cooper**, Prof. J., M.A., M.Sc.; Rhodes University College, Grahamstown, S. Africa.
E. **Orr**, M. Y.; Royal Botanic Gardens, Edinburgh.
E. **Osborn**, Prof. T. G. B.; University Dept. of Botany, High Street, Oxford.
E. A. **Park**, Dr O.; Zoological Dept., Northwestern University College of Liberal Arts, Evanston, Ill., U.S.A.
E. **Peace**, T. R., M.A.; Imperial Forestry Institute, Oxford.
A. **Peacock**, Prof. A. D., D.Sc., F.R.S.E.; University College, Dundee.
E. **Pearl**, R. T.; South Eastern Agricultural College, Wye, Ashford, Kent.
E. **Pearsall**, W. H., D.Sc.; Botany Dept., The University, Sheffield (*Hon. Editor of The Journal of Ecology*).
E. A. **Pearson**, J.; Tasmanian Museum and Art Gallery, Hobart, Tasmania.
E. A. **Pease**, I. E., The Hollins, Ramton, Northallerton.
A. **Pentelow**, F. T. K.; 8, Loughborough Road, West Bridgford, Nottingham.
A. **Percival**, E.; Canterbury College, Christchurch, New Zealand.
E. A. **Perthshire Soc. of Nat. Science** (Secretary, John Ritchie); Perthshire Soc. of Nat. Science Museum, Perth, Scotland.
E. **Petch**, C. P.; Sundial House, North Wootton, King's Lynn, Norfolk.
E. **Phillips**, Prof. J. F. V., D.Sc.; University of Witwatersrand, Milner Park, Johannesburg, Transvaal.
A. **Phillips**, P. G.; Box 605, Gallup, New Mexico, U.S.A.
A. **Pickles**, W.; 23, Beech Grove Avenue, Garforth, Leeds, Yorks.
E. **Piemeisel**, R. L.; P.O. Box 826, Twin Falls, Idaho, U.S.A.
E. **Pilling**, M., Ph.D.; Croft House, Outlane, Huddersfield.
A. **Pitt**, Miss F.; The Albynes, Bridgnorth, Salop.
E. **Pitt**, J.; c/o Forest Dept., Morogoro, Tanganyika Territory.
A. **Plomley**, N. J. B.; c/o Bank of New South Wales, 29, Threadneedle Street, London, E.C. 2.
A. **Pollitt**, G. P., Col.; Harrage Grange, Cressage, Shropshire.
E. **Polunin**, N., Ph.D.; Univ. Dept. of Botany, High Street, Oxford.
E. A. **Potts**, W. H., M.A.; Dept. of Tsetse Research, Shinyanga, Tanganyika Territory.
E. **Powell**, Miss Doris, M.Sc.; Aldersyde, Reigate, Surrey.
E. A. **Praeger**, Dr R. Lloyd; Royal Irish Academy, 19, Dawson Street, Dublin.
E. **Pratt**, Dr C. A.; Imperial College, London, S.W. 7.
E. **Price**, W. R.; Cockleford Mill, Cowley, Nr Cheltenham.
E. **Priestley**, Prof. J. H., D.S.O.; The University, Leeds.
E. **Ramsbottom**, J., M.A., O.B.E.; Botanical Dept., British Museum (Nat. History), London. S.W. 7.
A. **Ratcliffe**, F. N., B.A.; Nat. History Dept., Marischal College, Aberdeen.
E. **Rayner**, Dr M. C.; Bedford College, University of London, Regent's Park, London, N.W. 1.
E. **Rees**, J., B.A., B.Sc.; University College, Cardiff.
E. **Rees**, T. Kenneth; University College, Singleton Road, Swansea, S. Wales.
E. **Regel**, Prof. Constantin; The Botanical Garden, Kaunas (Kovno), Lithuania.
A. **Reid**, D. M.; Science Schools, Harrow-on-the-Hill, Middlesex.
E. A. **Renouf**, Prof. L. P. W.; University College, Cork, Eire.
E. **Rice**, C. H., B.Sc. Ph.D.; 20, Dyson Road, Leytonstone.
E. A. **Richards**, O. W., M.A., D.Sc.; 29 *a*, Edith Road, London, W. 14.
E. **Richards**, P. W.; The Botany School, Cambridge.
A. **Ritchie**, Prof. J., M.A., D.Sc.; Dept. of Zoology, The University, Edinburgh.

E. A. **Robbins**, Capt. C. R., M.C., M.A.; P.O., Box 2830, Johannesburg.
A. **Roberts**, B. B.; Bishopsgarth, Woking, Surrey.
A. **Roberts**, J. I.; Medical Research Lab., Box 141, Nairobi, Kenya Colony.
E. **Robertson**, R. N.; The Botany Dept., The University, Sydney, N.S.W.
E. **Rogers**, Miss M. H.; 23 *a*, Shakespeare Road, Bedford.
E. A. **Roi**, J., D.Sc.; Musée Hoang Ho Pai Ho, Racecourse Road, Tientsin, China.
E. **Ross**, R.; British Museum (Natural History), Cromwell Road, London, S.W. 7.
E. **Rübel**, Dr E.; Zürichbergstrasse 30, Zürich, Switzerland.
A. **Rushton**, W., D.Sc.; Biological Dept., St Thomas's Hospital Medical School, Albert Embankment, London, S.E. 1.
A. **Russell**, Dr E. S.; Dolphins, Northchurch Common, Berkhamsted, Herts.
E. **Russell-Wells**, Miss B., Ph.D.; Botany Dept., University College, London, W.C. 1.
E. **Sager**, J. L., M.A.; 5, Teneriffe Terrace, Exmouth, Devon.
E. A. **Salisbury**, Prof. E. J., F.R.S.; Willow Pool, Radlett, Herts.
E. **Sandwith**, N. Y., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Sangster**, R. G.; Assistant Conservator of Forests, P.O. Box 31, Entebbe, Uganda.
E. **Saunders**, Miss E. R.; 37 Millington Road, Cambridge.
E. A. **Saunders**, J. T., M.A.; Christ's College, Cambridge.
A. **Savage**, R. M.; 19, Derwent Avenue, London, N.W. 7.
E. **Schröter**, Prof. C.; Seegartenstrasse, Pensionscegarten, Zürich 8, Switzerland (*Hon. Life Member*).
A. **Scourfield**, D. J., I.S.O., F.L.S.; 6, Chadwick Road, Leytonstone, London, E. 11.
Selwood, Miss G. F.; 49, Blenheim Road, Moseley, Birmingham (*Associate Member*).
E. **Sernander**, Prof. R.; Vaxtbiologiska Institutionen, Upsala, Sweden.
A. **Severtzeff**, Dr S. A.; Zoological Museum, M.G.U., Moscow, U.S.S.R.
E. **Shantz**, Prof. H. L.; Forest Service, Washington, U.S.A.
E. A. **Shelford**, Prof. Victor E.; Experimental Zoological Laboratory, Wright and Healey Streets, Champaign, Ill., U.S.A.
E. **Sherrin**, W. R.; South London Bot. Inst., 323, Norwood Road, Herne Hill, London, S.W. 24.
E. **Shirk**, C. J., Ph.D.; Nebraska Wesleyan University, Lincoln, Nebraska, U.S.A.
A. **Shorrock**, W. G.; Morland Hall, nr Penrith, Westmorland.
E. **Singh**, Prof. B. N., D.Sc.; Institute of Agricultural Research, Benares Hindu University, Benares, India.
E. **Skene**, Prof. Macgregor, D.Sc.; The University, Bristol.
E. **von Soò**, Prof. Rudolf; Debrécen, Hungary.
A. **Southern**, H. N., B.A.; 67 Holden Road, Woodside Park, London, N. 12.
E. **Sprague**, T. A., D.Sc.; Royal Botanic Gardens, Kew, Surrey.
E. A. **Squire**, F. A.; Imperial College of Tropical Agriculture, Trinidad.
E. A. **Stamp**, Dr L. Dudley; London School of Economics, London, W.C. 2.
E. **Stapledon**, Prof. Sir R. G., M.A., C.B.E.; University College, Aberystwyth.
A. **Stephen**, Dr A. C.; Royal Scottish Museum, Edinburgh.
A. **Stephenson**, Prof. T. A., D.Sc.; The University, Rondebosch, Cape Town, S. Africa.
A. **Steven**, D. M.; Magdalen College, Oxford.
E. **Stevenson**, Miss E. H.; The Training College, The Close, Salisbury.
E. A. **Steward**, F. C., Ph.D.; Dept. of Botany, Birkbeck College, Bream's Buildings, Fetter Lane, London, E.C. 4.
E. **Stiles**, Prof. W., M.A., F.R.S.; The University, Birmingham.
A. **Storrow**, B., M.Sc.; Dove Marine Lab., Cullercoats, Northumberland.
E. **Summerhayes**, V. S., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew, Surrey (*Hon. Treasurer*).

E. **Swabey**, C.; Forest Department, Port of Spain, Trinidad, B.W.I.
A. **Swynnerton**, G. H.; c/o Messrs Grindlay and Co. Ltd., 54, Parliament Street, London, S.W. 1.
E. **Symington**, C. F.; Kepong, Selangor, Federated Malay States.
E. **Synge**, P. M.; Clare Cottage, West Byfleet, Surrey.
E. A. **Tansley**, Prof. A. G., F.R.S.; Grantchester, Cambridge (*President*).
A. **Tattersall**, Prof. W. M., D.Sc.; Zoology Dept., University College, Cardiff.
E. **Thoday**, Prof. D., M.A., Sc.D.; University College, Bangor, N. Wales.
E. **Thomas**, Dr Ethel Miles; University of London Club, Gower Street, London, W.C. 1.
E. **Thomas**, H. Hamshaw, Sc.D., F.R.S.; Botany School, Cambridge.
E. **Thompson**, Prof. J. McLean; Botanical Dept., The University, Liverpool.
E. **Tidmarsh**, C. E. M.; Clare College, Cambridge.
E. **Tincker**, M. A. H., D.Sc.; Royal Horticultural Society Gardens, Ripley, Wisley, Surrey.
E. **Topham**, P., M.A.; Dedza, Nyasaland, B.C., Africa.
E. A. **Trapnell**, C. G., B.A.; Department of Agriculture, Mazabuka, N. Rhodesia.
E. A. **Trowbridge**, A. H.; U.S. Dept. of Agriculture, Bureau of Biological Survey, Section of Food Habits Research, Washington, D.C., U.S.A.
A. **Tucker**, B. W., M.A.; 9, Marston Ferry Road, Oxford.
E. **Turner**, Prof. J. S., Ph.D.; Botany Dept., The University, Melbourne, Victoria.
E. A. **Turrill**, W. B., D.Sc.; Royal Botanic Gardens, Kew, Surrey.
E. **Tutin**, T. G., B.A.; 27 Bateman Street, Cambridge.
A. **Uéno**, M.; Otsu Biological Station of the Kyoto Imperial University, Shigaken, Japan.
E. **Ulehla**, Prof., V.; Institute of Plant Physiology, 63, Kaunicova, Masaryk University, Brno, Cesko-Slovenska.
A. **Uvarov**, B. P.; British Museum (Nat. History), London, S.W. 7.
E. **Valentine**, D. H.; The Botany School, Cambridge.
A. **Varley**, G. C., B.A.; Sidney Sussex College, Cambridge (*Hon. Secretary*).
E. **Vaughan**, R. E., B.Sc., A.R.C.S.; Royal College, Curepipe, Mauritius.
A. **Venables**, L. S. V.; The Moors, Tilford, Surrey.
E. **de Vesian**, Miss D. E.; Ladies' College, Cheltenham.
A. **Vevers**, H. G.; Magdalen College, Oxford.
A. **Vogt**, W.; 609, West 114th Street, New York City, U.S.A.
A. **Volterra**, Prof. V., D.Sc., LL.D.; Via in Lucina 17, Roma, Italy.
E. **Vyvyan**, M. C., M.A.; Trevedran, Wateringbury, Kent.
E. **Wadham**, Prof. S. M.; School of Agriculture, Melbourne University, Victoria, Australia.
A. **Waite**, Miss B. E.; Museum Cottage, Haslemere, Surrey.
A. **Waloff**, Miss N.; Clevelands, Benenden, Cranbrook, Kent.
E. **Walton**, Prof. J.; Dept. of Botany, The University, Glasgow.
E. **Warburg**, E. F., Ph.D.; Bedford College, Regent's Park, London, N.W. 1.
A. **Warwick**, T., B.Sc.; Royal (Dick) Veterinary College, Edinburgh.
E. **Watson**, W., D.Sc.; Cedene, Cheddon Road, Taunton, Somerset.
E. A. **Watt**, A. S., Ph.D.; The Botany School, Cambridge (*Hon. Treasurer*); receives subscriptions.
A. **Watt**, Hugh Boyd; 90, Parliament Hill Mansions, Lissenden Gardens, N.W. 5 (*Hon. Life-Member*).
E. A. **Weese**, Prof. A. O.; University of Oklahoma, Norman, Okla., U.S.A.
A. **Weiss**, Prof. F. E., F.R.S.; Easedale, Woodway, Merrow, Guildford.
A. **White**, K. M., B.Sc.; Glastonbury, Boyn Hill Avenue, Maidenhead.

E. **Wiehe**, P. O.; Floreal, Mauritius.

A. **Williams**, C. B.; Rothamsted Experimental Station, Harpenden, Herts.

E. **Wilmott**, A. J., M.A.; Botanical Dept., British Museum (Nat. History) London, S.W. 7.

E. **Woodhead**, Norman, M.Sc.; University College, Bangor, N. Wales.

E. **Woodhead**, Dr T. W.; The Willows, 35, Longley Road, Huddersfield.

E. **Wright**, N., A.R.C.S., B.Sc.; Imperial College of Tropical Agriculture, St Augustine, Trinidad, B.W.I.

A. **Yapp**, W. B., B.A.; The Grammar School, Rusholme, Manchester.

E. A. **Yoshii**, Prof. Y.; Inst. of Biology, Tohoku Imperial University, Sendai, Japan.

VOLUME 8 NOVEMBER 1939 No. 2

BIRD DISTRIBUTION ON THE SOUTH DOWNS, AND A COMPARISON WITH THAT OF SURREY GREENSAND HEATHS

BY L. S. V. VENABLES

(*With Plates* 8–9 *and* 1 *Figure in the Text*)

CONTENTS

	PAGE
1. Introduction	227
2. The botanical phases	229
(*a*) Chalk	229
Grass	229
Scrub	229
(*b*) Greensand	230
3. Discussion on bird distribution	230
(*a*) Chalk	230
General	230
Grass	231
Scrub	233
(*b*) Comparison with Greensand heaths	234
Comparison of botanical phases	234
Avifaunal comparison	234
4. Summary	236
References	237
Appendix: Plant names used in the text	237

1. INTRODUCTION

FROM east to west across the south-east counties of England runs a range of chalk hills known as the South Downs, which form one side of the jagged remains of a denuded chalk dome (Fig. 1). This southern side is wide enough to have been carved out into a bold array of steep-sided hills which run up to some 900 ft. above sea-level and stand well up from the intervening plain of Greensand heaths and the more fertile Wealden areas, between their abrupt northern scarp and the corresponding rise of the narrower North Downs. The hills are mostly flat-topped and frequently several miles in length.

It was on these downs that this investigation into bird distribution was conducted. From an ornithological viewpoint the plant associations were found to fall into eight main types (see below), and the bird distribution on each of these was studied. Woodland (mostly pine, oak and beech; pure or mixed) was not included, as such chalk hill woods have been dealt with in a general survey of British woodland birds (Lack & Venables, 1939).

The method used for obtaining the data given in Table 2 was that of

slowly walking a number of miles through each type and noting the birds seen. This not only showed which birds were occurring in which types but also, as the distance covered was recorded, afforded some basis for a rough quantitative comparison. The edge of any section, or places rapidly changing from one type to another in a short distance were avoided, it being an easy matter to find a large expanse of the same type (save in differentiating between open and closed scrub). A given grass phase would be found running along a hillside or hilltop for a considerable distance (Pl. 8, phot. 1), and the folds in these hills were not infrequently filled with patches of scrubland; though scrub was by no means confined to sheltered slopes.

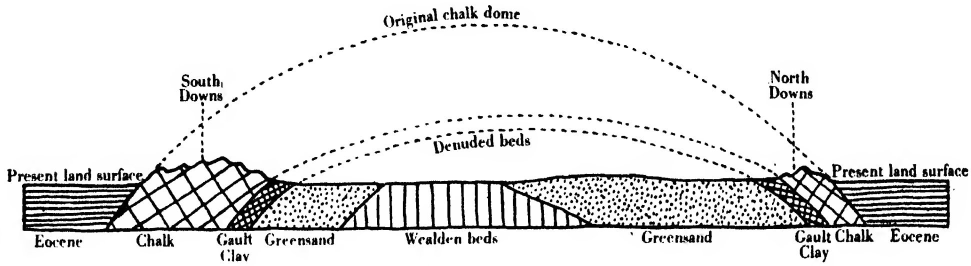


Fig. 1. Imaginary section through the Weald: the remains of the denuded chalk dome stand up in abrupt scarps. Vertical scale much exaggerated.

As this study is concerned with the breeding season only, the birds are dealt with—both in the tables and in the text—as pairs, never as single birds. In practically every case, however (except with game birds), this was checked in other ways, as by both birds being seen or heard, male in song, nest found, bird betraying much anxiety and thus presumably having a nest, and so on. For the sake of simplicity in the tables, single pheasants and cuckoos are also referred to as "pairs", although, in fact, the former is usually polygamous, and the latter usually polyandrous. Obvious non-breeders such as gulls, rooks, swifts, etc., were not counted.

The data given in Table 2 were obtained during the last few days of April and the first week in May 1938, and only at times of day and conditions of weather when the birds could be expected to be reasonably active and conspicuous. The walks were made between the Midhurst-Chichester road to the east and the Meon Valley to the west. Many points were checked and some of the juniper scrub was covered, however, later in May in the vicinity of Leckford, Hampshire (by kind permission of Mr J. Spedan Lewis); and, in previous years, visits had been paid to the Berkshire Downs and the Chiltern Hills.

Owing to the fact that the data in Table 2 were obtained in the early part of the spring, possibly such late migrants as turtle dove and nightjar were missed. I have found the nightjar breeding in open thorn-elder scrub on the Berkshire Downs, and Ingram & Salmon (1924) record the turtle dove as

being, under certain conditions, essentially a scrub-nester. However, the nightjar is very inconspicuous owing to its nocturnal habits, and the turtle dove at Leckford was confined almost entirely to the tallest hedgerows.

2. The botanical phases

(a) Chalk

These fall into eight main types which are as follows:

Grass. The grass on the hills is practically untouched by man: it is mostly grazed but not cut. The "cultivated" grass (fertilized, chain-harrowed and mown) in the valleys between the hills was avoided, because as natural a grass formation as possible was desired for the purpose of comparison with the natural heather heaths of Surrey Greensand. This hill grass was divided into three types:

(1) *Thick grass with occasional bushes* (Pl. 8, phot. 1). Grass mostly ankle deep with tufts up to knee height in places. Occasional scattered bushes of thorn, elder, yew or juniper. This is not unlike the well-known Savannah formation which is so extensive in many parts of the world.

(2) *Sparse grass with occasional bushes* (Pl. 8, phot. 2). Short-cropped turf, frequently with patches of bare earth and rabbit holes—the rabbits being one cause of the shortness of the turf. Tufts even ankle deep were rare. Occasional bushes as in (1).

(3) *Sparse grass*. As in (2), but without the bushes.

Scrub. As distinct from evenly planted man-made plantations, the scrub areas of the South Downs showed a good deal of variation—it was not common for a stand to be constant over any considerable area. An attempt was made to keep "Open" and "Closed" distinct, but this distinction must be somewhat arbitrary at times; closed stands had some parts open, and vice versa. Also, no stands in these "natural" areas were quite pure. The deciduous areas had a few definitely dominant species (these are given) and the evergreen areas had as well-marked dominants either yew or juniper. These were kept separate but it should be understood that a few deciduous bushes (frequently elder) were always present.

The height, too, was very variable—from young, low bushes up to 25 ft. or more in the case of the yew, and mostly 6–12 ft. with the juniper (Pl. 9, phot. 5). The thorn scrub ranged up to 15 ft., a few shrubs being taller and many shorter.

The ground vegetation of the scrub areas frequently varied too much in a small distance (i.e. in a single nesting territory) to make it possible to define it. As a general rule, however, evergreen scrub had sparse ground vegetation—often none in closed scrub; and deciduous frequently had good vegetation, though this varied in different places from short rabbit-cropped turf to rich patches of brambles and bracken.

(4) *Closed thorn scrub*. Thorn dominant (*Crataegus oxyacantha* and *Prunus spinosa*) with some elder, bramble and gorse in places. The bushes ranging up to 15 ft., a few taller and many shorter. Patchy ground vegetation (see above).

(5) *Open thorn scrub* (Pl. 8, phot. 3). As in (4), but in open formation.

(6) *Closed yew scrub* (Pl. 9, phot. 4). Dense yew with occasional admixture of other species. From young, low bushes up to 25 ft. or more. Mostly bare earth beneath but short grass in places.

(7) *Open yew scrub* (Pl. 9, phot. 4). Similar to (6) but in open formation. Frequently with a carpet of short grass.

(8) *Open juniper scrub* (Pl. 9, phot. 5). Very open formation of dominant juniper bushes; 6–12 ft. high with occasional seedlings. Sparse grass ground vegetation as in (2) and (3).

In the thick hedges of the cultivated valleys the lower part of the "scrub" was, on the average, much thicker than in the natural scrub stands of the hills. This difference was reflected in the avifauna of the dense, artificial hedge-scrub of the lowlands. The low-nesting yellow and cirl buntings were both more numerous than in the hills, and corn buntings (*Emberiza calandra*), too, were not uncommon though entirely absent from the downland counts. On the Berkshire Downs and at Leckford, however, I found them in typical type 1. (On the Berkshire Downs near Lambourne I have crossed a wide expanse of rich grass without any bushes. Jumps for training race-horses have been erected, however, and the corn bunting has come in as a breeding species, the males using the jumps as song-posts.) Some lesser whitethroats (*Sylvia curruca*) were seen at the valley hedgerows but none was encountered in the hill scrub though this species, too, was breeding in open thorn scrub (as type 5) on the Chilterns. The tall valley trees accounted for the presence there of tree pipits (see Venables, 1937).

(a) Greensand

For the purpose of comparing chalk and Greensand bird distribution some figures from typical Greensand scrub are appended. The greater density near the ground, especially in the gorse scrub, is reflected in the greater numbers of such birds as whitethroats that nest just above ground level.

(9) *Pine scrub.* Closed to open; very variable. 6–12 ft. pines with occasional gorse bushes and tall pine or birch trees. Heather ground vegetation; mostly thick and frequently knee high.

(10) *Gorse scrub.* Dense patches of gorse bushes up to 6 ft. high. Mostly thick, tall heather between, but bracken and grass in places. Occasional birch or pine trees.

(*Natural birch scrub.* The scattered patches of thin birch saplings afford little or no actual cover and apparently merely bring in the song post species (see Venables, 1937). Chaffinches and even, on rare occasions, nightingales breed in the thicker patches, but these were too small to afford a reasonable count.)

3. Discussion on bird distribution

(a) Chalk

It is not proposed to enter into a lengthy discussion here, as all the data are given in Table 2. Some of the more striking points are these:

General. Taken as a whole unit, the three grass phases showed a marked difference from the scrub phases. Not only had the former largely different species but a smaller variety and less birds per mile. This is to be expected,

Phot. L. S. V. Venables

Phot. 1. Type 1: Hill of thick grass with occasional bushes. Shows large expanse of single vegetation type.

Phot. L. S. V. Venables

Phot. 2. Type 2: Sparse grass with occasional bushes. Note the frequent patches of bare earth.

Phot. L. S. V. Venables

Phot. 3. Type 5: Open thorn scrub.

Table 1

	Chalk								Greensand	
Vegetation type ...	1	2	3	4	5	6	7	8	9	10
Description ...	Thick grass with bushes	Sparse grass with bushes	Sparse grass	Closed thorn scrub	Open thorn scrub	Closed yew scrub	Open yew scrub	Open juniper scrub	Pine scrub	Gorse scrub
Miles counted	6	7	6	3	4	4	3	3	3	3
Pairs per mile	20	13	12	43	42	24	27	14	12	22
Total number of species	8	15	6	20	21	16	20	12	12	14

as the grass phases had only one "layer" of habitat, so to speak, and the scrub phases more. The open juniper scrub is an exception, but this was so very open (Pl. 9, phot. 5) that it really was not very different from type 2 (sparse grass with occasional bushes, Pl. 8, phot. 2). A few scrub species came in with the scattered bushes of types 1 and 2, but not nearly so many as might have been expected. The converse was also true: much open scrubland had ground vegetation very similar to types 1, 2 and 3, but the typical birds of the latter phases (skylark, woodlark, meadow pipit, wheatear, stone-curlew and lapwing) were not found there (except in open juniper scrub). If nest site, nest material and food were the only limiting factors there appears to be no ecological reason, save possibly that of food, why a bush-nester could not nest in a single bush on a large expanse of grass, and no reason at all why a ground-nesting "moorland" bird could not nest in a small grass patch in scrub. The psychological aspect of bird distribution has been discussed by Lack (1933), Lack (1937), Lack & Venables (1937) and Venables (1937). It would seem that not only must each individual species have its special nest site, but the actual appearance of the territory as a whole must "look right". Table 2 shows that it was rare for a bush-nester or -singer to be found breeding where there was not a great number of bushes (i.e. scrub), and for a ground-nester and air-singer to nest where there was not a big expanse of grass and much open air space immediately above it.

Grass. The thick grass had a higher density of birds than the sparse grass phases, but the latter, together, had a greater variety of species. The habitat selection of some birds was very marked. The meadow pipit was numerous in the thick grass (seven pairs to the mile), but only one pair was seen in 13 miles of sparse grass. The skylark nested freely in sparse grass but was twice as numerous in thick grass. Conversely, there were seven pairs of lapwings to the mile in sparse grass but only one pair was found in 6 miles of thick grass; the six pairs of stone-curlew and the 20 pairs of wheatears were all in the sparse grass and none in the thick; and the four pairs of woodlarks all in sparse grass with song posts. These figures include the open juniper scrub where an overlap community was found. The scattered bushes of types 1 and 2 introduced only a very few bush birds: all were less than one to the mile.

Vegetation type	Chalk (grass)						Chalk (scrub)										Greensand (scrub)			
	1 Thick grass with bushes		2 Sparse grass with bushes		3 Sparse grass		4 Closed thorn scrub		5 Open thorn scrub		6 Closed yew scrub		7 Open yew scrub		8 Open juniper scrub		9 Pine scrub		10 Gorse scrub	
Miles counted	6		7		6		3		4		4		3		3		3		3	
	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs
Carrion crow (*Corvus corone*)	.	.	.	.	.	.	**1**	2	**×**	1	**×**	2	**×**	1	.	.	.	.	.	.
Magpie (*Pica pica*)	.	.	.	.	.	.	**1**	3	**×**	2	**1**	4	**1**	3	.	.	.	.	.	.
Greenfinch (*Chloris chloris*)	.	.	.	.	.	.	**×**	1	**1**	3	.	.	**×**	1	**2**	6	.	.	.	.
Chaffinch (*Fringilla coelebs*)	.	.	**×**	2	.	.	**8**	23	**8**	33	**6**	25	**8**	28	**3**	10	**2**	5	**×**	1
Linnet (*Acanthis cannabina*)	**×**	2	**×**	1	.	.	**2**	5	**2**	6	**1**	3	**3**	8	**2**	6	.	.	**2**	6
Yellow bunting (*Emberiza citrinella*)	**1**	4	.	.	.	.	**×**	1	**1**	4	.	.	**×**	1	**1**	2	**×**	1	**1**	2
Cirl bunting (*Emberiza cirlus*)	.	.	.	.	.	.	**×**	1	.	.	.	.	.	.	.	.	.	.	.	.
Skylark (*Alauda arvensis*)	**10**	59	**3**	23	**5**	29	.	.	.	.	.	.	.	.	**1**	3	.	.	**×**	1
Woodlark (*Lullula arborea*)	.	.	**×**	3	.	.	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.
Tree pipit (*Anthus trivialis*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	3	**1**	2
Meadow pipit (*Anthus pratensis*)	**7**	40	**×**	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Goldcrest (*Regulus regulus*)	.	.	.	.	.	.	.	.	.	.	**2**	8	**2**	6	.	.	**×**	1	.	.
Great tit (*Parus major*)	.	.	.	.	.	.	**×**	1	**×**	2	**×**	2	**1**	3	.	.	.	.	.	.
Coal tit (*Parus ater*)	.	.	.	.	.	.	.	.	.	.	**1**	5	.	.	.	.	**×**	1	.	.
Marsh tit (*Parus palustris*)	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.	.	.	.	.	.	.
Willow tit (*Parus atricapillus*)	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.	.	.	.	.	.	.
Blue tit (*Parus caeruleus*)	.	.	.	.	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.	.	.
Whitethroat (*Sylvia communis*)	.	.	.	.	.	.	**1**	3	**2**	8	.	.	.	.	.	.	**1**	2	**8**	25
Blackcap (*Sylvia atricapilla*)	.	.	.	.	.	.	**×**	1	.	.	.	.	.	.	.	.	.	.	.	.
Dartford warbler (*Melizophilus undatus*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	4	**1**	3
Willow warbler (*Phylloscopus trochilus*)	.	.	**×**	1	.	.	**8**	25	**9**	35	**1**	4	**1**	2	.	.	**4**	13	**3**	8
Chiffchaff (*Phylloscopus collybita*)	.	.	.	.	.	.	.	.	.	.	**×**	1	**×**	1	.	.	.	.	.	.
Mistle thrush (*Turdus viscivorus*)	.	.	.	.	.	.	**1**	3	.	.	.	.	.	.	.	.	.	.	.	.
Song thrush (*Turdus ericetorum*)	.	.	.	.	.	.	**1**	4	**2**	6	.	.	**×**	1	.	.	.	.	.	.
Blackbird (*Turdus merula*)	.	.	**×**	2	.	.	**8**	23	**7**	27	**3**	12	**4**	11	**2**	6	.	.	**1**	2
Robin (*Erithacus rubecula*)	.	.	.	.	.	.	**5**	16	**4**	16	**4**	15	**3**	9	.	.	**1**	3	**1**	2
Nightingale (*Luscinia megarhyncha*)	.	.	.	.	.	.	.	.	**×**	2	.	.	.	.	.	.	.	.	.	.
Stonechat (*Saxicola torquata*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**×**	1
Wheatear (*Oenanthe oenanthe*)	.	.	**2**	11	**1**	7	.	.	.	.	.	.	.	.	**1**	2	.	.	.	.
Dunnock (*Prunella modularis*)	.	.	.	.	.	.	**2**	6	**2**	8	**1**	4	**1**	2	.	.	**1**	2	**2**	6
Wren (*Troglodytes troglodytes*)	.	.	.	.	.	.	**1**	2	**×**	1	**×**	1	**×**	1	.	.	.	.	**1**	3
Green woodpecker (*Picus viridis*)	.	.	.	.	.	.	.	.	**×**	1	**×**	1	.	.	.	.	.	.	.	.
Cuckoo (*Cuculus canorus*)	**1**	5	**1**	6	**×**	2	.	.	**1**	4	.	.	**×**	1	**1**	2	**×**	1	**1**	3
Little owl (*Athene noctua*)	.	.	**×**	1	**×**	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Kestrel (*Falco tinnunculus*)	.	.	.	.	.	.	**×**	1	.	.	.	.	.	.	.	.	.	.	.	.
Stone curlew (*Oedicnemus oedicnemus*)	.	.	**×**	3	**×**	2	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.
Lapwing (*Vanellus vanellus*)	**×**	1	**4**	29	**5**	29	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stock dove (*Columba oenas*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.
Ring dove (*Columba palumbus*)	.	.	.	.	.	.	**2**	7	**1**	4	**2**	9	**1**	3	.	.	.	.	.	.
Pheasant (*Phasianus colchicus*)	**×**	3	**×**	1	.	.	**1**	2	**1**	3	**×**	1	**×**	1	.	.	**×**	1	.	.
Red-legged partridge (*Alectoris rufa*)	.	.	**×**	2	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.	.	.
Common partridge (*Perdix perdix*)	**1**	5	**×**	3	.	.	.	.	.	.	.	.	.	.	**×**	1	.	.	.	.

Scrub. As in evergreen *versus* deciduous woodland, the evergreen scrub had a lower density of population than the deciduous. The variety of species, however, was about the same but slightly less for closed yew. This, perhaps, is not surprising, the dense foliage (Pl. 9, phot. 4) causing a dark, gloomy interior with little cover save in the thickly interlocking canopy, while of ground vegetation there was little or none. An interesting point is that in this, the tallest formation, the chiffchaff came in as a breeding species, whereas the closely allied willow warbler was well distributed throughout all the scrub. As is pointed out by Lack & Venables (1939) the former species demands a higher song post than the latter.

The goldcrest and, to a lesser extent, the coal tit were quite common in yew but absent from thorn. Lack & Venables (1939), show that this is also true of woodland; the goldcrest especially predominating in conifer, i.e. evergreen woods. On the other hand the willow warbler and, to a smaller extent, the blackbird were a good deal more numerous in the deciduous scrub. The ubiquitous chaffinch ranged in more or less equal numbers through them all.

Only small patches of closed juniper scrub were found during the census taking; these were too small and uncommon to give a reasonable amount of data. Lack & Venables (1939), however, give some figures for a stand of 4–10 ft. juniper bushes, dense in places, near Salisbury. The birds found there, in numerical order of observed frequency, were chaffinch, blackbird, willow warbler, goldcrest, yellow bunting, cirl bunting, linnet, song thrush, dunnock (hedge sparrow) and little owl. This list agrees well with the species seen in the small patches during the present investigation and it would seem that closed juniper scrub is, as regards its avifauna, much the same as closed yew scrub, if one takes into consideration the comparatively lower and smaller bushes of the former.

The scrub community had a considerable overlap with what are usually considered woodland species, showing that the large trunks and branches are not really necessary for such birds: the make-up and, presumably, general appearance of a scrub stand of bushes sufficing. The canopy-nesting carrion crow, magpie and kestrel; the lower-nesting ringdove; and the hole-nesting green woodpecker and tits, all featured in the counts; but Lack & Venables (1939), in discussing British woodland, say that in this country at the present day, with the almost complete lack of natural stands of trees and bushes, it is very difficult to differentiate between woodland and scrubland species. The data given in Table 2 show that the latter community embraces many species usually met with nowadays in the vicinity of large trees only. As, of course, there were less holes suitable for tits in the scrub bushes than in big trees, so too there were correspondingly less tits. It is perhaps not surprising that the green woodpecker was the only woodpecker encountered in this scrub. It seems to be forsaking woods and becoming a ground-feeder. It is only logical, therefore, that it should forsake large trees for nesting.

Lack and myself have already discussed the psychological points of habitat selection and their influence on bird distribution. These points include such features as the high post demanded by some species for the male to sing from—although perhaps not demanded by a closely allied species; the apparent inability of an individual species to breed save in a certain type of nest in a certain type of place, while there is usually no apparent physical reason; the preference for sparse ground vegetation of some ground-nesters, and for thick of others, and so on.

(b) Comparison with Greensand heaths

In a previous contribution to the subject of bird distribution (Venables, 1937) it was pointed out that the birds there described should be studied in another environment and the distributional limiting factors in the two places compared. It was in part for this reason that distribution on chalk hills was investigated in 1938. Environmentally, both situations have much in common —dry soil with a ground vegetation rich, moderate, or almost absent; and single bushes or patches of scrub. Both are more or less natural communities and very little interfered with directly by man.

Comparison of botanical phases. These have already been described for the Surrey Greensand heaths (Venables, 1937) but are briefly summarized against the similar chalk hill phases as follows:

Greensand, phase 1. Bare earth after fire. A parallel to this was not seen on the chalk.

Greensand, phase 2. Patchy vegetation, frequently short, and patches of bare earth. This is much the same as types 2 and 3 of the chalk—sparse grass with patches of bare earth, and with or without scattered bushes. The bushes on chalk type 2 are alive and would do for a bush-nester, but those on Greensand phase 2 are fire-killed and would do as song posts only.

Greensand, phases 3 and 4. 3 is moderate heather growth and 4 is rich (18 in. tó 2 ft.) heather with bushes and saplings standing well up. These two may be taken roughly to equal chalk type 1; rich grass, ankle deep with knee-high tufts, and scattered bushes.

The scrub stands, on the other hand, are a good deal different in that both the Greensand types (gorse and pine) have a rich ground vegetation of full-grown heather and the gorse is dense from ground level right up to the top. On the chalk, the thorn scrub has good ground vegetation in places and sparse in others, while the latter is generally poor in open juniper and open yew, and very frequently completely absent in closed yew.

Avifaunal comparison. The following species occurring both on chalk downs and Greensand heaths have, as far as possible, similar habitats:

Carrion crow. Nest built in a tree on Greensand and in the tallest scrub (thorn and yew) on chalk.

Chaffinch. Bush or tree for nesting and song post. Occurred in small numbers with scattered bushes but very numerous in scrubland on both chalk and Greensand.

Linnet. As the last, save that much of the singing takes place in company or while flying about and appears to have almost no territorial significance (see Tucker, 1938).

Yellow bunting. Thick lower vegetation for nesting, and a song post—chalk and Greensand.

Phot. L. S. V. Venables

Phot. 4. Types 6 and 7: Closed yew scrub in foreground; open yew scrub behind.

Phot. L. S. V. Venables

Phot. 5. Type 8: Open juniper scrub.

Table 3

	Greensand		
	Phase	Scrub type	Chalk type
Carrion crow	1–4	.	4–7
Chaffinch	4	9–10	2 4–8
Linnet	4	10	1–2 4–8
Yellow bunting	4	9–10	1 4–5 7–8
Skylark	2–4	10	1–3 8
Woodlark	1–3	.	2 8
Meadow pipit	4	.	1–2
Goldcrest	.	9	6–7
Coal tit	.	9	6
Whitethroat	4	9–10	4–5
Willow warbler	3–4	9–10	2 4–7
Blackbird	.	10	2 4–8
Wheatear	1–3	.	2–3 8
Dunnock	.	9–10	4–7
Wren	.	10	4–7
Cuckoo	3–4	9–10	1–3 5 7–8
Kestrel	2–4	.	4
Stock dove	1–4	.	8
Pheasant, Red-legged partridge, Common partridge	See context		

Skylark. The fondness for grass (see Lack & Venables, 1937) is well shown in the chalk figures, as is also the fact that this species was quite numerous on even sparse vegetation with patches of bare earth, as in the heathland habitats. It was common in thick grass (chalk) as it was found to be in codominant grass and heather (Greensand).

Woodlark. Sparse or patchy ground vegetation with a song post—chalk and Greensand.

Meadow pipit. Thick ground vegetation for nesting—chalk and Greensand. There were seven pairs to the mile on the thick grass of type 1 (chalk), but only one pair in 13 miles of sparse grass. On Greensand, all the 86 territories analysed were in phase 4.

Goldcrest. In the best stands of evergreen scrub—chalk and Greensand.

Coal tit. As the last, but none seen in open yew.

Whitethroat. A scrub species requiring thick lower vegetation for nesting—chalk and Greensand. This stand was most typical of type 10, and here the whitethroat was most numerous with eight pairs to the mile. The figures show a marked avoidance of evergreen scrub.

Willow warbler. Bush or tree for song post, and ground vegetation for nesting—chalk and Greensand. Nine pairs to the mile in seven miles of chalk thorn scrub, four pairs to the mile in six miles of Greensand pine and gorse scrub, all having good or moderate ground vegetation, but only one pair to the mile in seven miles of chalk yew scrub with its sparse undergrowth.

Blackbird. Well distributed throughout all chalk scrub. Two pairs in the gorse scrub on Greensand but none in the pine scrub.[1] Two pairs were seen in 13 miles of grass with occasional bushes.

Wheatear. Both on chalk and Greensand the limiting factors were sparse or absent ground vegetation, and a rabbit hole for nesting. Of the twenty pairs seen during the chalk down walks, all were on sparse grass types (see discussion in Venables, 1937, p. 84).

Dunnock. In all the scrub types, chalk and Greensand, except the very open juniper scrub.

Wren. Thinly distributed throughout the denser scrub—chalk and Greensand. The two thinnest types (chalk open juniper and Greensand pine) being avoided.

Cuckoo. More or less evenly distributed where it could get a good look-out place and

[1] After this was written, a breeding pair was found in Greensand pine scrub.

where there were plentiful nests of small Passerines—chalk and Greensand. Dense, closed scrub was avoided.

Kestrel. Tree for nesting on Greensand, substituted by tall scrub on chalk.

Stock dove. A hole-nester, tree or ground, on Greensand. Only one pair seen during the chalk counts; presumably nesting in a rabbit hole.

Pheasant, red-legged partridge and common partridge. The habitats on Greensand were analysed by the finding of nests or by some sound indication that the nests were there. They were all on phase 4 with its dense ground vegetation for concealing eggs. During the walks across chalk downland no nests of these species were found; the birds recorded in Table 2 being the non-incubating ones scattered over various types. The "woodland" species (the pheasant) was usually in scrubland, and the partridges mostly on open grassland.

The only markedly dissimilar species, common to both formations, was the *lapwing*. On both chalk and Greensand, sparse (also absent in the case of the latter) ground vegetation was chosen for nesting. On Greensand one pair was found on phase 3, twelve on phase 2 and nineteen on phase 1. On chalk, fifty-eight pairs were found in 13 miles of sparse grass, and only one pair on six miles of thick grass. On Greensand, however, they were all found breeding not far from marsh or water while on the chalk they were, of necessity, up in the high, dry hills.

It will be seen how closely the birds common both to Greensand heaths and chalk downland have parallel habitats on both formations. Thick grass is used instead of the rich heather growth, and sparse grass instead of the poor ground vegetation found for the first few years after a heath fire. The gorse patches and thickets of young pine on heathland are used successfully in place of the deciduous and evergreen scrub stands on the chalk hills. Nevertheless, these differences in flora would seem to be of some importance, as a number of species are found on one or other of the formations but not on both.

(Compare Table 2 in the present communication with Table 2 in Venables, 1937.)

4. Summary

1. The distribution of breeding birds (determined by walking counts) on the chalk hills known as the South Downs is described, and compared with that of Surrey Lower Greensand heaths.

2. The plant associations on the chalk downs are divided into eight main types; three of grass, two of deciduous scrub, and three of evergreen scrub.

3. There is a short general discussion on the bird distribution, followed by a more detailed one on the grass types and then on the scrub types. The complete data are given in Table 2.

4. The general succession of the ground vegetation on the Greensand heaths is compared, so far as possible, with the grass types on the chalk. The two main Greensand heath scrub formations are described for the purpose of comparison with those on chalk. The species of birds occurring on both places are discussed individually.

5. As far as practicable with the different flora, the birds are found to choose much the same habitats both on chalk hills and on Greensand heaths.

REFERENCES

Lack, D. (1933). "Habitat selection in birds...." J. Anim. Ecol. 2: 239–62.

Lack, D. (1937). "The psychological factor in bird distribution." Brit. Birds, 31: 130–6.

Lack, D. & Venables, L. S. V. (1937). "The heathland birds of South Haven Peninsula, Studland Heath, Dorset." J. Anim. Ecol. 6: 62–72.

Lack, D. & Venables, L. S. V. (1939). "The habitat distribution of British woodland birds." J. Anim. Ecol. 8: 39–71.

Ingram, G. C. S. & Salmon, H. M. (1924). "The turtle-dove in Glamorganshire." Brit. Birds, 18: 1–10.

Tucker, B. W. (1938). In WITHERBY, H. F. and others, "The handbook of British birds". London, 1: 79.

Venables, L. S. V. (1937). "Bird distribution on Surrey Greensand heaths: the avifaunal-botanical correlation." J. Anim. Ecol. 6: 73–85.

APPENDIX

Plant names used in the text

Beech	*Fagus sylvatica*	Heather	*Calluna vulgaris* and *Erica cinerea*
Birch	*Betula* sp.	Juniper	*Juniperus communis*
Bracken	*Pteridium aquilina*	Oak	*Quercus* sp.
Bramble	*Rubus* sp.	Pine	*Pinus* sp. (mainly *sylvestris*)
Elder	*Sambucus nigra*	Sloe (Blackthorn)	*Prunus spinosa*
Gorse	*Ulex europaeus*	Yew	*Taxus baccata*
Hawthorn	*Crataegus oxyacantha*		

THE ANALYSIS OF AN ANIMAL POPULATION

By C. H. N. JACKSON

(*With* 1 *Figure in the Text*)

CONTENTS

		PAGE
1.	Introduction	238
2.	Estimation of the population	239
3.	The "negative" method	241
4.	Death-and-emigration and birth-and-immigration	242
5.	Death and birth	244
6.	Error of the population estimate	245
7.	Summary	245
8.	Acknowledgements	246
	Reference	246

1. Introduction

In a previous paper (Jackson, 1936) an account was given of the estimation of a tsetse-fly population through the year by means of the "Lincoln Index". Since then certain amendments have become necessary as the mathematical treatment has improved, and the method has been extended to provide estimates of rates of birth, death and dispersal which were previously unobtainable. It is the purpose of this paper to explain and describe these improvements and extensions, as the use of the method seems potentially of wide application in problems of animal ecology.

The principle is simple. A random sample of individuals is marked: at some later time a random sample is caught and examined: either the initial marking or the later catching is done evenly over the area selected for study. The second catch includes a certain proportion of individuals recognized by their marks as having been caught in the first sample. Then, subject to conditions considered below, the proportion of recaptures to total taken in the second catch ought to be the same as the proportion initially marked to the total population. That is, the population is equal to

$$\frac{\text{total marked} \times \text{total caught when recapturing}}{\text{recaptures}}.$$

For closed areas, this formula gives good results when the breeding and non-breeding seasons are well defined and when neither is overlapped by the interval between marking and recapturing. For other conditions modification is necessary.

One assumption and some general principles must be stated. The assumption is that no individuals dealt with in an experiment must be any more likely than any others of the species to show themselves to the catchers on

the recapture day. Thus if one sex or one age group of the animals is more willing to appear and be caught, that sex or group must be separately considered throughout. When the activity of the animals determines their readiness to be caught, and when individuals overlap each other in their activity periods, marking or recapturing must be continued long enough, or the interval between them must be made long enough, to damp out the effect of periodic individual activity. For example, if an individual animal is likely to be active about every second day, those marked on any one day are either more or less likely than those unmarked to be seen on the day following. To counteract this, we must either mark on two consecutive days and recapture later, or mark all on one day and recapture on two days, or after many.

Whenever, as must often be necessary, the interval between marking and recapturing is not negligibly short, the formula must be modified to deal with animals whose generations overlap or which, between marking and recapturing, move into or out of the area selected for study. This is because the proportion of marked to unmarked individuals will diminish between marking and recapturing through death or emigration of some of the marked individuals, and their replacement by others being born or hatched, or entering the area from outside.

But if the environmental conditions are not exceedingly inconstant, the proportion of marked to unmarked individuals will decrease in a fairly regular way (actually in geometrical progression) with the passage of time after the marking date: and by taking samples at regular intervals after marking we can estimate the rate of decrease of the marked proportion. Once this is known, we are able to estimate what the proportion was on the date of marking, and so apply the formula already given. Even with a relatively inconstant environment, a smooth "die-away" curve can be obtained by taking averages of single curves, and reliable estimations of the population can be made.

2. ESTIMATION OF THE POPULATION

The data here considered are drawn from studies in Africa on the tsetse-fly *Glossina morsitans* Westwood, and refer only to males which had had their first feed and were therefore not recognizably young. The marking area was a square with sides 4 miles long; and for the purpose of estimating dispersal rate (see below) it was subdivided into quarters each of 4 sq. miles. The flies were marked at weekly intervals, actually on the first 3 days of every week, evenly throughout the square, the four marking parties avoiding any definite paths. The marking was altered weekly, and every quarter-square was distinguished by a separate mark.

The method has already been explained (1936) but must be recalled to assist the understanding of subsequent sections of this paper. The number of individuals caught and marked at regular intervals will probably vary from

date to date. The first step, therefore, is to correct the recaptures as if some constant number (say 100) had been marked, and the same number caught on every recapture date. For example:

Marked	Caught on recapture dates					
1582	1547	1307	603	1081	1261	1798
	Recaptures					
	103	82	24	31	10	11

The first corrected figure (y_1) will be $\frac{103 \times 100 \times 100}{1582 \times 1547}$, the second ($y_2$) will be $\frac{82 \times 100 \times 100}{1582 \times 1307}$, and so on. When all six have been corrected in this way, they become:

y_1	y_2	y_3	y_4	y_5	y_6
0·4207	0·3966	0·2574	0·1812	0·0501	0·0387

What we require to find from the above series is y_0, which we will call a, the corrected figure which would have been obtained had we been able to recapture on the date of marking. For this purpose, we must first find r, the common or average ratio of each value of y to the value preceding it, or of y_1 to a. For general purposes r can be calculated from the formula

$$r = \frac{y_2 + \dots + y_k}{y_1 + \dots + y_{k-1}}.$$

But Mr W. L. Stevens has lately shown that when, as in our example, $k = 6$, a more accurate estimate is:

$$r = \sqrt{\frac{y_3 + y_4 + y_5 + y_6}{y_1 + y_2 + y_3 + y_4}},$$

which in the example given works out to 0·6480. To find a we calculate

$$a = \frac{y_1 + \dots + y_{k-1}}{r} - (y_1 + \dots + y_{k-2}),$$

which for this example

$$= \frac{y_1 + \dots + y_5}{r} - (y_1 + \dots + y_4)$$

$$= 0{\cdot}759.$$

Now since all the values of y, and therefore that of a, have been corrected as if 100 were marked and 100 caught on every recapture date, and since the population formula is (see above)

$$\frac{\text{total marked} \times \text{total caught when recapturing}}{\text{recaptures}},$$

the population in the present instance will clearly be

$$\frac{100 \times 100}{a} = 13{,}200 \text{ approximately.}$$

To summarize this calculation:

(i) Correct all the recaptures as if 100 had been marked initially and 100 caught on all recapture dates.

(ii) Take the sum of all but the first two.

(iii) Divide by the sum of all but the last two.

(iv) Take the square root, thus finding r.

[1](v) Take the sum of all but the last one.

[1](vi) Divide by r.

[1](vii) Subtract the sum of all but the last two, to find a.

(viii) Divide into 10,000 to get the population.

Average estimates of population on several recapture dates may be made either by averaging the respective values of y_1, and y_2, etc., and calculating a from the result, or by averaging values of a calculated from separate recapture curves. The alternative method given on pp. 853–4 of the paper quoted above is more troublesome and seems to be less accurate, not more accurate as there stated.

3. The "negative" method

This also was described in 1936 (p. 854). In the "positive" treatment exemplified in the last section, we considered recaptures in subsequent catches of flies marked on a certain date. We can equally well consider recaptures on a certain date from flies marked in previous catches. This treatment I have called the "negative" method (Fig. 1). Both methods ought to give nearly the same value of a for any particular date. For example:

Caught	Marked on previous dates					
1558	1183	1198	1401	1299	1086	1262
	Recaptures					
	70	48	28	17	5	1
	Corrected recapture figures					
	0·3798	0·2569	0·1283	0·0840	0·0296	0·0051

Proceeding exactly as before, we find r to be 0·5394, from which we calculate $a = 0{\cdot}780$, which divided into 10,000 gives a population estimate of about 12,800.

These two examples are drawn from actual field data, and refer to the same date. It will be seen that the two population estimates, 13,200 and 12,800, are not very discrepant. (It will be observed that the number "caught" in the second example is lower than the number "marked" in the first, whereas they should normally be equal. This is because 24 individuals, being still recognizably young when marked, were admissible as flies "marked" but not as flies "caught": any recovered a week later would have had their first meal, and would therefore be normal mature male flies.)

[1] Or, take the sum of all, divide by r, and subtract the sum of all but the last one.

4. Death-and-emigration and birth-and-immigration

We may use r_+ for the common ratio found by the "positive" method, and r_- for the common ratio by the "negative" method. Also, let

$$P = \text{population} = \frac{10{,}000}{a},$$

$D+E$ = death-and-emigration rate,

$B+I$ = birth-and-immigration rate,

n = the date for which the population is worked, by the "positive" method.

By "survival" is meant survival of flies still living in the marking area.

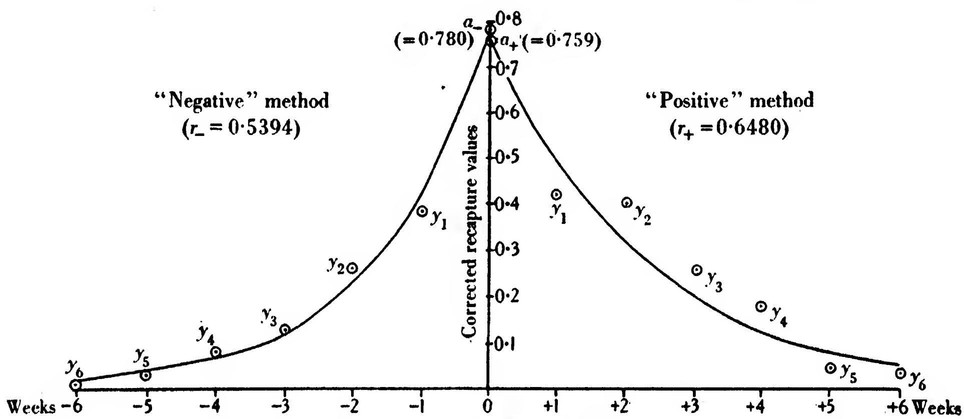


Fig. 1. Illustration of the calculation of the extrapolated points (a) by the "positive" and "negative" methods. All values are taken from the example in the text. The agreement between a_+ and a_- is not usually so close as in this example.

Of flies marked on any date, n, and recaptured on the following date of catching, $n+1$, the survival rate per fly if the whole population were seen on the recapture date would be the actual, uncorrected recaptures divided by the number marked. But we do not see the whole population, P_{n+1}, on the date$_{n+1}$, and the actual survival rate is

$$\frac{\text{recaptures}}{\text{number marked}} \times \frac{P_{n+1}}{\text{number caught date}_{n+1}}.$$

Since the corrected recapture figures, y, are those which should have been obtained had 100 been marked or caught on every date, we can write the above expression equal to

$$\frac{(y_1)_n}{100}\,\frac{P_{n+1}}{100}$$

$$= \frac{(y_1)_n}{a_{n+1}}.$$

This being the survival rate per fly, the death-and-emigration rate per fly is

$$D+E=1-\frac{(y_1)_n}{a_{n+1}},$$

which for smooth curves is the same as

$$1-r_-,$$

where r_- is r_- calculated for the date $n+1$.

To find the birth-and-immigration rate we argue as follows:

From date$_n$ to date$_{n+1}$ there die or leave the area

$$P_n(1-r_-).$$

Therefore there remain in the area from date$_n$

$$P_n-P_n(1-r_-).$$

Therefore there enter, or are hatched or born

$$P_{n+1}-[P_n-P_n(1-r_-)]$$
$$=\left[1-\left(\frac{P_n}{P_{n+1}}r_-\right)\right](P_{n+1})$$

which is a rate per fly of

$$B+I=1-\left(\frac{P_n}{P_{n+1}}r_-\right)$$
$$=1-\left(\frac{a_{n+1}}{a_n}r_-\right)$$

which for smooth curves is the same thing as

$$1-\left(\frac{a_{n+1}}{a_n}\frac{(y_1)_n}{a_{n+1}}\right)$$
$$=1-\frac{(y_1)_n}{a_n}$$
$$=1-r_+.$$

We have seen that the death-and-emigration rate per fly is $1-r_-$, and the birth-and-immigration rate is $1-r_+$. The dates to which these estimates refer, however, are not the same as the date for which the population was calculated, but are removed from it by a time equal to the mean interval between marking and recapture of all the recaptured flies used in the estimation of r. When r is about 0·6, as in the example given above, this time is between $1\frac{1}{2}$ and 2 intervals from the date for which the population was estimated.

In that example, the values of r by the "positive" method and by the "negative" method respectively were 0·6480 and 0·5394. The birth-and-immigration rate is therefore 0·3520 and the death-and-emigration rate is 0·4606. These values refer respectively to from $1\frac{1}{2}$ to 2 intervals (dates) after and before the date for which the population was calculated.

5. Death and birth

We now require to separate death from emigration and birth from immigration. This may be done if the marking area is in the form of a square divided into quarters. Since the periphery[1] of any of the small squares is half that of the large square containing them, the emigration rate from the large square, E, is about half that from the small squares, $2E$. The death-rate, D, is obviously the same in both.

Let r' be the common ratio for the small squares. Then

$$D+2E=1-r'_-,$$

$$D+E\ =1-r_-,$$

whence by subtraction $\quad E=r_- - r'_-,$

and again by subtraction $\quad D=1-2r_-+r'_-.$

Similarly $\quad I=r_+-r'_+$

and $\quad B=1-2r_++r'_+.$

In the foregoing example we saw that r_+ was 0·6480 and therefore $1-r_+$ was 0·3520. For the same date the recaptures of flies retaken in the same small squares as those in which they were marked were, at successive intervals, 73, 60, 13, 20, 8, 4. The number marked and the numbers caught in the weeks of recapture are of course the same in the four small squares combined as in the whole square, and the recaptures therefore are corrected to 0·2982, 0·2902, 0·1362, 0·1169, 0·0401, 0·0141.[2] From these values of y' the value of $1-r'_+$ is found to be 0·3958. Therefore we have

$$B+2I=0{\cdot}3958$$

$$B+I=0{\cdot}3520$$

$$I=0{\cdot}0438 \text{ or } 4\,\%$$

$$B=0{\cdot}3082 \text{ or } 31\,\%.$$

The death-rate is calculated in a similar way from r_- and r'_-. The length of life can be found by taking the reciprocal of the death-rate, $1/D$, which then gives length of life in units equal to the interval between marking and recapture dates. This length of life is the average which would occur if the death-rate remained unchanged, and is the same as the expectation of life at the time when the young fly becomes adult.

[1] Prof. R. A. Fisher informs me that dispersal rate varies, approximately, inversely as the periphery, provided the dispersal is fairly small.

[2] It may be observed that extrapolation of a from this series gives a higher population estimate than that for the whole square. This is because of the circumstances of the experiment, in which the markers temporarily accentuated the normal movement of animals within the large square. The results given are not thereby disturbed.

6. ERROR OF THE POPULATION ESTIMATE

On p. 853 of the other paper, a very complicated formula is given for the standard error of a. The values of A in this formula are correction fractions for the numbers marked, namely, 10,000 divided by the product of the number marked and the number caught on the recapture date. Where s is the standard error of a,

$$s^2=\frac{a}{r^4}[(2-r)^2r^2A_1r+(1-r)^4(A_2r^2+\ldots+A_{k-2}r^{k-2})+(1-2r)^2A_{k-1}r^{k-1}+A_kr^k].$$

Since r is a fraction, the first term in the bracket is much the largest, and provided the values of A are not very unequal we may write all values of $A=A_1$, when the formula becomes simply

$$s^2=aA_1f(r).$$

For any value of k, $f(r)$ can be calculated once and for all for a sufficient range of values of r, and the labour of calculating the standard errors is then very greatly reduced. In practice, this approximation has been found to change the estimate of s by only about 2% of the value found by the full formula, and is of special use in the design of experiments. For $k=6$, values of $f(r)$ have been worked to three decimal places for values of r from 0·35 to 0·80 (Table 1).

Table 1

Table of

$$\log\left\{\frac{1}{r^4}[(2-r)^2r^3+(1-r)^4(r^2+r^3+r^4)+(1-2r)^2r^5+r^6]\right\}$$

for values of r from 0·35 *to* 0·80

r	$f(r)$	r	$f(r)$	r	$f(r)$	r	$f(r)$	r	$f(r)$
—	—	0·41	0·873	0·51	0·700	0·61	0·567	0·71	0·477
—	—	0·42	0·855	0·52	0·686	0·62	0·557	0·72	0·471
—	—	0·43	0·837	0·53	0·670	0·63	0·547	0·73	0·467
—	—	0·44	0·819	0·54	0·656	0·64	0·537	0·74	0·461
0·35	1·006	0·45	0·800	0·55	0·643	0·65	0·526	0·75	0·455
0·36	0·979	0·46	0·780	0·56	0·629	0·66	0·518	0·76	0·451
0·37	0·960	0·47	0·764	0·57	0·616	0·67	0·508	0·77	0·447
0·38	0·934	0·48	0·748	0·58	0·603	0·68	0·499	0·78	0·445
0·39	0·915	0·49	0·730	0·59	0·591	0·69	0·490	0·79	0·441
0·40	0·895	0·50	0·714	0·60	0·579	0·70	0·486	0·80	0·438

Mr Stevens has lately shown that when $k=6$ this formula is only about 80% efficient when $r=0·6$, and the efficiency varies slightly for other values of r. Differences between values of a should not therefore be regarded as "significant" unless they exceed about 2¼ times their standard errors.

7. SUMMARY

A mathematical technique is described by which, under certain conditions, the absolute number of animals in a population can be calculated from the percentage of marked animals recaptured. This technique forms a development

of the idea of the "Lincoln Index", and makes allowance for the factors of birth, death, and migration onto and off the area studied. It is illustrated by field data obtained from tsetse fly populations in East Africa.

8. Acknowledgements

I am very grateful to Prof. R. A. Fisher, F.R.S., and to Mr W. L. Stevens, of the Galton Laboratory, London, for their interest and invaluable help at all stages of this work.

REFERENCE

Jackson, C. H. N. (1936). "Some new methods in the study of *Glossina morsitans*." Proc. Zool. Soc. Lond. 811–96.

CANADIAN ARCTIC WILD LIFE ENQUIRY, 1937–38[1]

By DENNIS CHITTY

Bureau of Animal Population, Oxford University

(*With 4 Figures in the Text*)

1. Introduction

This is the third annual report on replies to zoological questionnaires sent out by the Northwest Territories Administration, Ottawa, and by the Hudson's Bay Company. The forms ask for opinions on the abundance of certain animals during one year ending 31 May compared with the one before it. The government form is concerned with lemmings (*Lemmus* and *Dicrostonyx*), the arctic fox (*Alopex lagopus*), snowy owl (*Nyctea nyctea*) and ptarmigan (*Lagopus*) and with disease in sledge dogs. The Company's form goes to posts outside the Arctic as well, and, with the exception of ptarmigan, covers these animals and certain others. The object of the enquiry is to maintain a current record of some of those changes in animal numbers which are such a remarkable feature of the Arctic. It is hoped to define the years and the areas in which these fluctuations occur and to compare the different variables.

Sledge dogs are subject to various diseases, some of them perhaps contracted from wild animals such as the arctic fox. For this reason reports on the health of sledge dogs are being studied together with the cycle in Arctic wild life; and conditions further south are being followed for comparison.

There were 35 replies to questionnaires sent out by the Northwest Territories Administration. This material has been collected and forwarded for analysis in the Bureau of Animal Population through the good offices of the Commissioner of the Northwest Territories, Dr Charles Camsell, and the Deputy Commissioner, Mr R. A. Gibson. 70 reports were received from Hudson's Bay Company posts in the Arctic and Subarctic, and other posts supplied information on sledge dogs. The Fur Trade Commissioner in Winnipeg, Mr Ralph Parsons, and his staff, with the permission of the Governor and Committee of the Hudson's Bay Company, have kindly placed these annual zoological reports at the disposal of the investigation.

2. Methods

The data from each year's enquiry are condensed and reproduced as far as possible without distortion of the original replies, and irrespective of their apparent merit. The reader is thus in possession of all the information on

[1] Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

which the report is based and may see both the possibilities and limitations of the questionnaire method.

In Table 1 are given the opinions of observers about comparative and absolute abundance of arctic foxes, lemmings, "mice" and snowy owls. (The data on ptarmigan are being reserved.) These replies are arranged in a general order east to west or south to north and are divided into a number of rather arbitrary groups. Table 2 shows for each species (except "mice") how opinions as to their relative abundance are distributed within these groups.

The areas described in Table 1 have been plotted on a map from which Figs. 1, 3 and 4 have been constructed. All the areas reporting *increase* have been covered with arrows pointing up, these being spaced out, where a pattern can be made, at half-inch intervals on a map of 100 miles to an inch. Similarly the areas reporting *decrease* or *no change* have been indicated by arrows pointing down or horizontally. These symbols translate into diagrammatic form the comparisons listed in Table 1. They also (1) provide a means of making a very rough estimate of the percentage area covered by each kind of reply (i.e. one arrow $\doteqdot$ 2500 sq. miles), and (2) show where there is disagreement. A method of expressing these two aspects was evolved and explained in the first two reports, and the figures were found to agree remarkably well with those compiled from the number of observers. In view of this, and of the approximations involved in the area method (at any rate under the particular conditions of this enquiry) it is now felt that not much additional information is obtained by counting the arrows.

The previous reports should be consulted for a discussion of the species and of method. Some of the details with additional notes are given here:

(1) *Areas.* The wild life enquiry is confined to the groups described in Table 1 and does not include the Mackenzie River valley or, in the case of lemmings, group 3, and the south parts of groups 1 and 10. Areas are mapped as described, except where, as indicated by square brackets in Table 1, places were not located or the area seemed too far outside the breeding or migratory range of a species. A difficulty in this connexion is that observers often describe only one area for several species without indicating to what part of it some of them are limited. In these cases the area is listed in Table 1 as described, but not always mapped in full. As a rule, however, the replies are accepted without corrections.

(2) "*Mice.*" This column in Table 1 is given to supplement the information on lemmings, as the various species of wild mice and voles are also of importance as food for predators. The data are not at present used in the analysis, but it should be realized that there is likely to have been confusion among some observers in distinguishing between lemmings and "mice".

(3) *Count of observers.* There are three difficulties in making Table 2. Observers may (*a*) give different opinions for different parts of their area, or (*b*) times of the year, or (*c*) describe an area overlapping more than one of the arbitrary groups. With (*a*) the vote is divided; with (*b*) the opinion given for the year as a whole is counted: events at particular times are simply listed in Table 1; with (*c*) an observer's vote is counted only in the one group containing either his headquarters or the largest portion of the area.

(4) *Fort McKenzie.* This report is listed in group 2 but not included in the totals. It may

Table 1. *Summary of original data on arctic fox, lemming, snowy owl and sledge dog (part) for* 1937–38

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, s. = scarce, × = not noticeably scarce or abundant, a. = abundant, v. = very.

Sledge dogs: 0 indicates a report that disease was entirely absent. 0* = report of disease in minor proportions, + = more serious disease; details in Table 3 (*a*). One symbol is given each observer except where indicated (2), etc.

Square brackets indicate observations that have been partly or entirely omitted from either the map or the calculations—see text for explanation.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

	Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
Group 1. Northern Labrador coast					
Frenchman's Island, outside islands and 20 miles inland ...	D. s.	[I. a.]	I. a.	I. a.	0
Cartwright and 50 miles radius ...	I. s.	—	I. a.	I. a.	0
Rigolet, south 50, north 75, west 35 miles	I. s.	I. s.	I. ×	I. ×	—
Northwest River [and inland 400 miles, by trappers' reports] ...	I.	—	I.	—	—
Makkovik, 30 miles north and south [and inland, north-west, 100 miles from coast] ...	I. ×	—	I. ×	I. a.	0
Hopedale and 30 miles radius ...	I. ×	—	I. a.	I. ×	0
Davis Inlet and 30 miles radius ...	I. ×	—	I. a.	I. ×	0
Voisey's Bay, north-east 108, north 85, north-west and south-west 40 miles ...	I. a.	I. a.	I. a.	I. ×	—
Nain, 35 miles radius and north-west 70 miles ...	I. ×	I. a.	I. a.	I. ×	—
Nutak ...	I. ×	I. ×	I. a.	N. ×	0
Hebron and from Sedlik Bay to Napartok Bay ...	I. ×	I. v.s.	I. v.s.	I. a.	0
Spring ...	—	v.a.	v.a.	—	—
Port Burwell, Killinek Island and mainland within 100 miles ...	I. s.	I. a.	D. s.	I. a.	0*
Group 2. Coast of Northern Quebec, south to Richmond Gulf and inland					
Georges River and 50 [to 150] miles radius ...	I. v.s.	I. v.a.	I. v.a.	I.	—
Whale River to Georges River ...	I. s.	I. a.	I. a.	I. s.	—
Georges River, inland, *April* ...	v.a.	—	—	—	—
Fort Chimo and 25 miles radius ...	I. ×	I. ×	D. v.s.	I. ×	—
[Fort McKenzie and 120 miles radius]	[I. v.s.]	[D. v.s.]	[D. s.]	—	—
Leaf River, Leaf Bay and coastal area 40 miles east ...	—	I. a.	I. v.a.	I. ×	—
Early winter ...	D. ×	—	—	—	—
Payne Bay to Payne Lake; south 25, north 35 miles ...	D. ×	I. ×	—	D. s.	—
Fall ...	a.	—	—	—	—
Diana Bay: from Cape Hopes Advance in the north to within 30 miles of the Payne River in the south; west to a line from Burgoyne Bay to the Payne River	D.	D. s.	D. v.s.	D. ×	—
After Christmas ...	v.s.	—	—	—	—
Stupart Bay to East Sugluk and Burgoyne Bay ...	v.s.	I. v.a.	D. v.s.	D. v.s.	—
Sugluk West and 80 miles radius ...	I.	I.	—	I.	—
Late spring ...	v.a.	v.a.	—	v.a.	—
Wolstenholme; east to within 20 miles of Sugluk, south 72 miles to Kovik River	I. v.a.	I. v.a.	I. v.a.	D. v.s.	—
Spring ...	[D.]	—	—	—	—

Table I (*continued*)

	Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
Cape Smith, inland 50, south 20 and north 70 miles	I. a.	I. ×	—	I. ×	—
January–May	[D.] ×	—	—	—	—
Povungnetuk and 40 miles radius	I. a.	I. s.	I. a.	—	—
Port Harrison, north to Koklak River, south to Nastapoka River	I. ×	I. ×	I. ×	I. ×	—
28. Port Harrison, and from Kogatuk Bay to Broughton Island	I.	I. ×	—	D. ×	0
Middle of November–May	—	—	—	v.s.	—
Group 3. South parts of Hudson Bay, James Bay and inland					
Belcher Islands	I. s.	[D. s.]	—	I. a.	0
Spring	—	—	—	[D.] s.	—
Great Whale River north to Richmond Gulf, south to Cape Jones	I. a.	[I. a.]	I. a.	D. s.	+
Fort George and 100 miles radius	I. ×	[N.]	—	v.s.	—
Kanaapuscow, north and south 100; east [250] miles, west to coast	I. ×	[D. ×]	N. ×	N. ×	—
Eastmain, north 60, south 20, inland 150 miles	I. s.	—	I. a.	I. s.	—
Neoskweskau and 50 miles radius; [Nitchequon and 50 miles radius]	I. s.	—	I. ×	—	—
Albany	—	—	I. a.	—	—
November	—	—	D.	—	—
Kapisko north to Lawashi River, south 6 miles along coast, inland 6 miles along Kapisko River	—	—	I. a.	N. ×	0
Attawapiskat, south to the Lawashi River, 150 miles inland, north to Cape Henrietta Maria. Also Agamiski Island	D. s.	—	I. v.a.	N. ×	0
Lake River to 30 miles south of North Lawashi River, as far inland on all rivers as Opinega Lake and north to Trout River	N. ×	—	N. a.	N. ×	—
Weenusk, along the coast north 100, south 50 and inland [200] miles	I. ×	—	I. a.	N. ×	—
Severn, along the coast north-east to Kaskatamagan, south-east to Weenusk and inland [half-way to Trout Lake]	I. ×	—	D. s.	D. s.	0
York Factory, north 100 miles, east to Kaskatamagan, inland [almost to Shamattawa]	I. ×	—	N. ×	N. ×	+
Group 4. West coast of Hudson Bay, north from Nelson River					
Churchill, Seal River, North River, and along coast	I. ×	D. v.s.	D. v.s.	N. ×	—
Caribou; from Seal River to Big River (north and south 70 miles); east 40 and west 30 miles	I. a.	—	I.	D. s.	0
Nonala and 50 miles radius	D. ×	D. ×	D. ×	D. ×	—
Early fall. On the sea ice *in March*	v.a.	—	—	—	—
15. Lat. 59°–61°. Long. 97°–102°	D.	I.	—	D. v.s.	0
20. Lat. 60°–61° and from Nueltin Lake to within 50 miles of Hudson Bay coast	I. s.	D. v.s.	—	N. s.	0
Nueltin Lake to Ennadai Lake	N.	—	D. s.	N.	0
Winter	—	D. s.	—	—	—
Eskimo Point, west to edge of bush, north to Maguse River, south to Big River	N. ×	D. ×	D. ×	D. ×	0
North-west of post	I.	—	—	—	—
South of post. On coast *until late spring*	s.	—	—	—	—

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
12.	Eskimo Point	N.	N.	—	N.	0
	Padley and 8 miles radius	I. ×	D. ×	D. ×	—	0
	Tavane and 30 miles radius	I. a.	N. ×	I. a.	N. ×	0
	On coast edge	v.s.	—	—	—	—
	Chesterfield to Cape Fullerton; south to Rankin Inlet and 100 miles inland ...	I.	D. s.	—	D. s.	0
	Baker Lake, Beverly Lake and Kazan River (Group 4); Back River (Group 9)	I. ×	N. ×	—	D. s.	0
	Group 5. Southampton Island, Repulse Bay and Melville Peninsula					
	Repulse Bay, north-west to Committee Bay, east at Lyon Inlet, north at Igloolik and its vicinity on Melville Peninsula	I. a.	I. a.	—	—	0
	Spring	—	[D.] v.s.	—	—	—
	Southampton Island (whole island) ...	I. ×	I. ×	N. ×	N. ×	—
	Group 6. Southern Baffin Island					
	Lake Harbour east to Gabriel Strait, west to Fair Ness	I. ×	I. ×	—	I. ×	—
	Winter	—	[D.] v.s.	—	v.s.	—
32.	Lake Harbour district and south coast from Frobisher Bay to Foxe Channel	I.	I. ×	—	D. v.s.	0*
	Late spring	—	[D.] v.s.	—	—	—
	Cape Dorset and Foxe Peninsula ...	I.	I. ×	—	D. s.	—
	Frobisher Bay (post) and from Cape Haven round the bay to Newell Sound	I. ×	I. ×	—	D. s.	—
	February–March	[D.] v.s.	—	—	—	—
	Pangnirtung: mainly coastal observations in Cumberland Sound, Hoare Bay and due north on Davis Strait ...	I. ×	I. ×	—	I. ×	—
30.	Pangnirtung Fjord, Cumberland Sound and south to north shore of Frobisher Bay	I. ×	I. ×	—	N.	0
	Group 7. Northern Baffin Island and north					
	Clyde River to Coutts Inlet and Home Bay	I. ×	I. ×	—	I. ×	0*
	Early fall	v.a.	—	—	—	—
31.	Pond's Inlet, south to Home Bay, south-west to Igloolik, north to Lancaster Sound; south shore Bylot Island ...	I. a.	N. v.a.	—	I. v.a.	0
	Spring	—	[D.]	—	—	—
	Pond's Inlet, Eclipse Sound and Navy Board Inlet	I. ×	D. ×	—	D. ×	—
	Arctic Bay to Elwin Inlet and end of Admiralty Inlet	—	—	—	D. s.	—
	As above and Agu Bay	I. v.a.	—	—	—	—
33.	Craig Harbour, Ellesmere Island ...	I. ×	N. v.s.	—	—	0
	Group 8. Boothia Peninsula and islands west and north					
	Fort Ross, Boothia Peninsula and Somerset Island	I. ×	I. ×	—	—	—
	King William Island (Group 8), Adelaide Peninsula and east to Pelly Bay (Group 9)	I. v.a.	N.	—	I. v.a.	0
	Cambridge Bay to Wellington Bay, and Albert Edward Bay (Group 8); Coast of Kent peninsula on Dease Straits (Group 9)	I. ×	I. a.	—	—	0

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge Dog
35.	Cambridge Bay west to Wellington Bay, east to King William Island taking in shores of all islands (Group 8); White Bear Point to Cape Alexander (Group 9)	I. ×	I. v.a.	—	v.s.	—
	West of Cambridge Bay to Wellington Bay and Perry River to [Gjoahaven], King William Island	—	—	—	—	0
	Reid Island to Lady Franklin Point and to north shore of Prince Albert Sound	I. ×	I. v.a.	—	I. ×	—
19.	Minto Inlet	v.s.	v.s.	—	D. v.s.	0
	May	a.	[I.] v.a.	—	—	—
	Fort Collinson and east and west shore of Prince of Wales Strait	D. ×	I. ×	—	N. ×	—
	Group 9. Pelly Bay, west to east of Coppermine River, and inland to Back River					
	Bathurst Inlet: west coast from Wollaston Point south to Western River and inland 100 miles; east coast from Gordon Bay to Western River and inland 50 miles. Also Lakes Finnie and Beechey	N. ×	N. ×	I. ×	—	0
8.	100 miles south of East Kugaryuak River (roughly 10 miles east of White Sandy River)	v.s.	—	—	—	0
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
	Stony Rapids, 150 miles north of ...	—	[I. ×]	N. ×	D.	—
	April (especially)	I. ×	—	—	—	—
	Snowdrift and between Lat. 61°–64° and Long. 106°–112°	N. s.	N. ×	N. ×	D. s.	0
	East of Long. 107° *in spring*	[I.]	—	—	—	—
5.	Fort Reliance	—	N.	—	—	0*
	Fort Resolution and 40 miles radius ...	I. ×	—	N. ×	—	0
2.	Ptarmigan Lake, Clinton Colden Lake	I. ×	I. ×	—	N. s.	0
	Fort Reliance	—	—	—	—	0
6.	Lac de Gras, south to Outram Lakes ...	D. v.s.	N. s.	—	N. s.	0
29.	Headwaters of Coppermine, Lakes Providence and de Gras	N. v.s.	I. v.a.	—	N. s.	0
23.	Yellowknife mining district	—	D. s.	D.	I. s.	0
	Fort Rae, south-east 80 miles to Yellowknife River [north-west 150 miles to end of Lac La Marte, north-north-west 180 miles to Lake Grandin], approx. north 150 miles to Lake Hardisty and 150 miles north-east to end of Snare Lake	N. s.	I. a.	I. a.	—	0
	Group 11. Coppermine River to Alaska					
21.	Coppermine Settlement and 12 miles up river to Bloody Falls	N. v.s.	N. v.s.	—	N. v.s.	0
18.	Dismal Lakes District	I.	I.	—	I.	0
16.	North-east shore of Great Bear Lake ...	—	I. v.a.	—	—	0
25.	From Cape Krusenstern 50 miles west and south to Rae River	I. ×	N.	I.	I. v.a.	—
	Krusenstern and Basil Bay; also Lady Franklin Point	—	—	—	—	0 (2)
34.	South shore of Beaufort Sea between Long. 122° and 133°	I. ×	D. ×	—	D. ×	0
	Baillie Island, south-east 60, south 70 miles	I. ×	I. a.	—	I. a.	—
	Spring	v.s.	[D.]	—	—	—

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
3.	Mackenzie Delta and coast between Herschel and Baillie Islands	N. ×	I. v.a.	—	I. ×	—
	Forts Norman, Good Hope and McPherson; Aklavik	—	—	—	—	+ (4)
	Tuktuk, south to south of Kittigazuit, east to Kugalook, north to Cape Dalhousie, west to Richards Island ...	D. ×	—	I. a.	—	0
22.	Mackenzie R. delta, East Branch, and Richards Island	D. v.s.	I. v.a.	—	—	—
	As above and east to Eskimo Lakes ...	—	v.a.	—	D. v.s.	—
	Aklavik to [Point Separation and] Shingle Point	D. s.	D. ×	D. ×	D. ×	+
	Shingle Point to Demarcation Point, about 130 miles	D.	N. ×	—	—	0

be regarded as a subdivision of group 2 subject to rather different conditions from those on the coast.

(5) *Sledge dog.* Only one symbol is placed on the map (Fig. 2) for each area, except where two or more distinct places are named. A circle (at the centre or headquarters of the area) indicates a report of disease absent or in very minor proportions; a plus sign is given where more serious disease or an epidemic was reported. Absence of disease (or of sledge dogs) may also be inferred at the Hudson's Bay Company posts in Table 1 from which no statements were received; though these posts are not distinguished on the map.

3. RESULTS

By 1935–36 decrease to great scarcity had occurred among all species. In the following year conditions improved in the Eastern Arctic, particularly on the north coast of Quebec and in Baffin Island. In the Western Arctic little recovery was apparent. In 1937–38 lemmings and snowy owls increased on the coast of the Quebec peninsula and in parts of the Western Arctic, but started to decrease in Baffin Island. Recovery continued among arctic foxes in the east and started on the islands and parts of the coast further west.

Lemming. From Rigolet in Labrador round the coast of the Quebec Peninsula to Port Harrison in Hudson Bay, lemming reports were of increase at all places except Diana Bay. (There seems also to have been a considerable increase among "mice".) Reports of increase on this coast have risen from 3 out of 15 (1935–36) through 10 out of 19 (1936–37) to 18 out of 19 (1937–38). On the west coast of Hudson Bay about half the observers in both 1935–36 and 1936–37 thought that lemmings were increasing; but during 1937–38 only 1 out of 11 held this view. From Repulse Bay, Southampton Island and all of southern Baffin Island increase was reported; but in the Repulse Bay and Lake Harbour districts there were reports of decrease in the latter half of the period, and a similar report came from Northern Baffin Island.

In the Western Arctic there seems to have been an improvement in lemming numbers on Boothia Peninsula, Somerset Island, Victoria Island and from

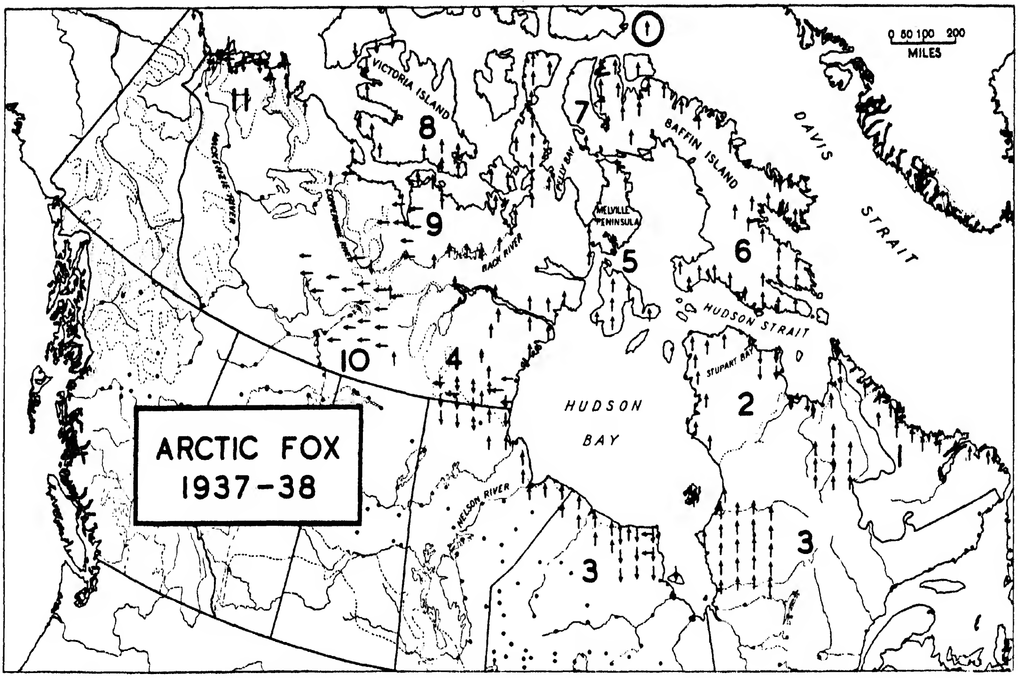


Fig. 1. State of the arctic fox population in 1937–38 compared with 1936–37. Arrows indicate the areas covered by observers reporting Increase (↑), Decrease (↓), and No change, not abundant (←). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset Craig Harbour, Ellesmere Island.

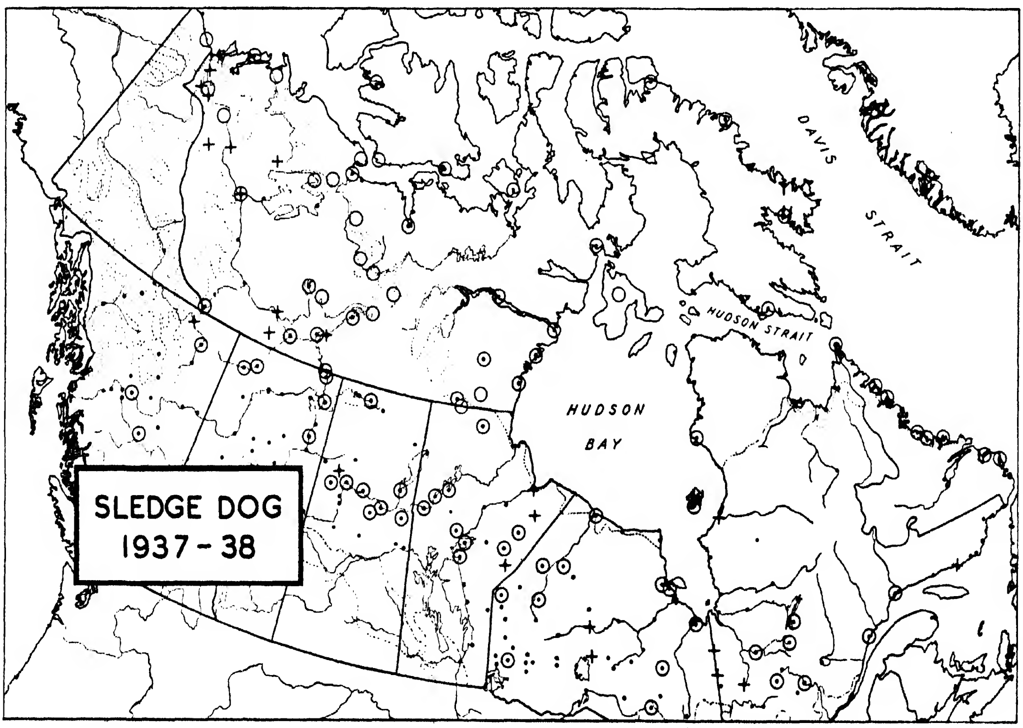


Fig. 2. Prevalence of disease among sledge dogs in 1937–38. Reports of disease are indicated +; disease absent or in minor proportions 0. Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones.

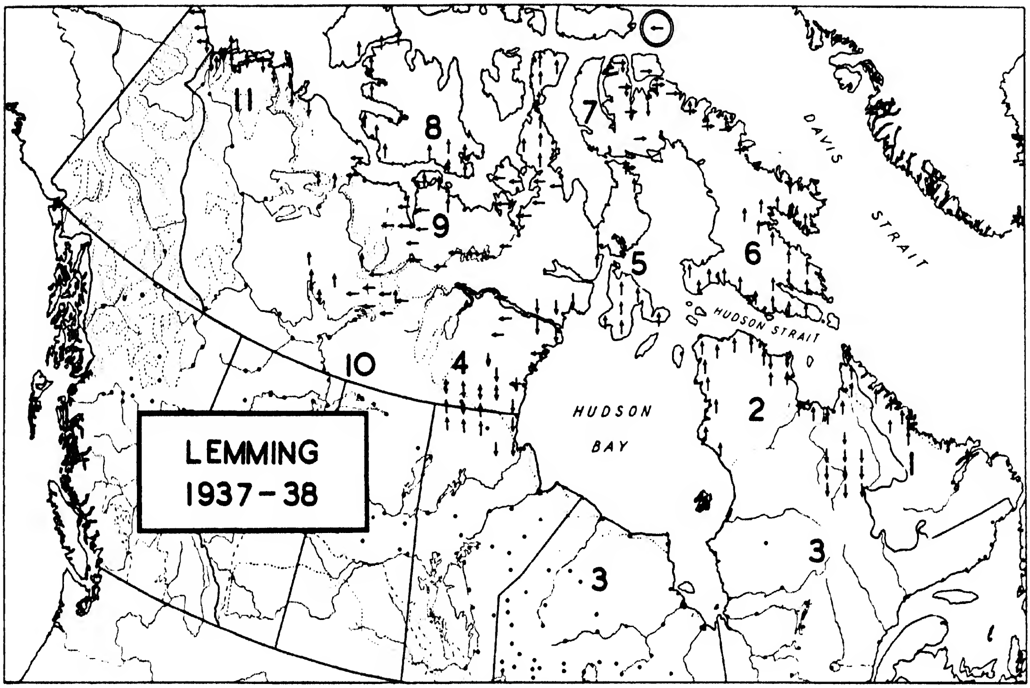


Fig. 3.

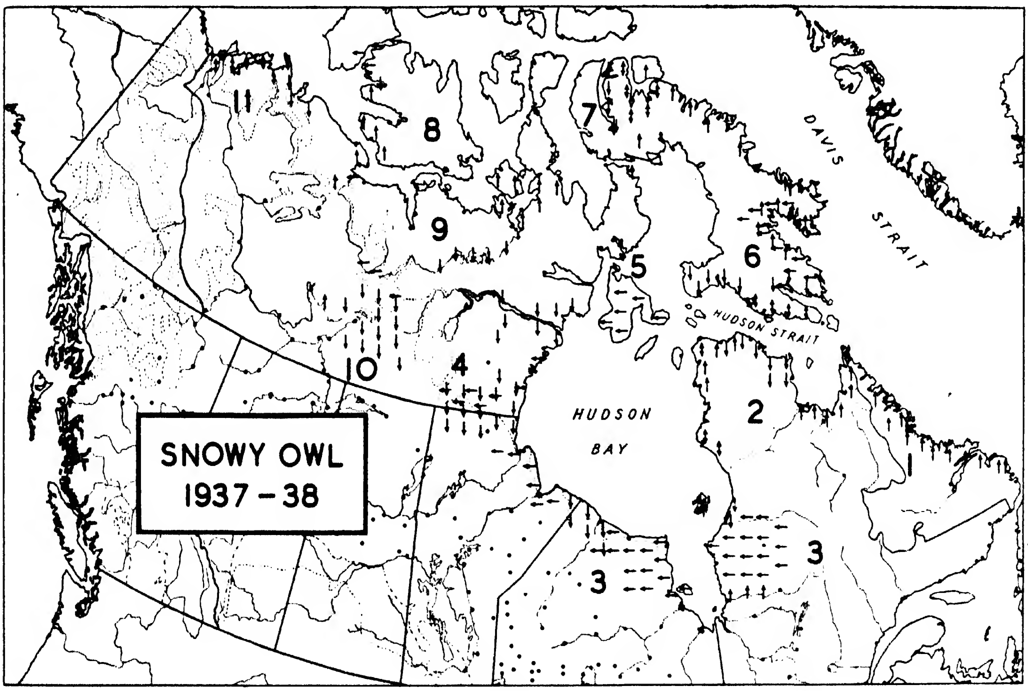


Fig. 4.

Figs. 3, 4. State of the lemming and snowy owl populations in 1937-38 compared with 1936-37. Arrows indicate areas covered by observers reporting Increase (↑), Decrease (↓), and No change, not abundant (←), No change abundant (→). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

Baillie Island to the Mackenzie delta. In places the start of this upward swing had been observed in 1936–37. Inland from Back River and Bathurst Inlet no significant trend in the lemming population has become apparent during 1935–38.

Table 2. *State of arctic fox, lemming and snowy owl populations in* 1937–38. *Number of observers reporting relative abundance compared with* 1936–37

	Eastern Arctic								
Group no. ...	1	2	3	4	5	6	7	Total	%
Arctic fox:									
Increase	11	9	9	7½	2	6	5	49½	**82**
Decrease	1	3	1	2	—	—	—	7	**12**
No change	—	—	1	2½	—	—	—	3½	**6**
	12	12	11	12	2	6	5	60	**100**
Lemming:									
Increase	6	12	—	1	2	6	1	28	**67**
Decrease	—	1	—	7	—	—	1	9	**21**
No change	—	—	—	3	—	—	2	5	**12**
	6	13	—	11	2	6	4	42	**100**
Snowy owl:									
Increase	10	7	2	—	—	2	2	23	**42**
Decrease	—	5	2	6	—	3	2	18	**33**
No change	1	—	6	5	1	1	—	14	**25**
	11	12	10	11	1	6	4	55	**100**

	Western Arctic					
Group no. ...	8	9	10	11	Total	%
Arctic fox:						
Increase	5	—	3	4	12	**50**
Decrease	1	—	1	4	6	**25**
No change	—	1	3	2	6	**25**
	6	1	7	10	24	**100**
Lemming:						
Increase	5	—	3	5	13	**54**
Decrease	—	—	1	2	3	**13**
No change	1	1	3	3	8	**33**
	6	1	7	10	24	**100**
Snowy owl:						
Increase	2	—	1	4	7	**39**
Decrease	1	—	2	3	6	**33**
No change	1	—	3	1	5	**28**
	4	—	6	8	18	**100**

Arctic fox. From Cartwright to Port Burwell and west to Fort Chimo all observers reported an increase in arctic foxes. This was a decided improvement on the two years 1935–36 and 1936–37, when respectively 1 out of 12 and 4 out of 13 reports of increase were received. In 1936–37 increase was reported all the way from Leaf River to Port Harrison. This trend was only partly maintained in 1937–38, as from Leaf River to Stupart Bay decrease or great scarcity was reported. A decided improvement is shown by the figures for increase in group 3, which in three years have risen as follows: 0 out of 10, 3 out of 9, 9 out of 11. The increase in groups 1 and 3 (largely outside the breeding range) is probably because of southward movements: the result of increased populations further north. The majority of reports were of increase

over the following huge circuit: from Churchill up the west coast of Hudson Bay and inland; north-east to the tip of Melville Peninsula; the islands of Southampton, Baffin, Ellesmere, Somerset, Victoria and King William; south of Dease Strait, in Adelaide and Boothia Peninsulas, Back River, to Baker Lake. Of the 31 observers in these regions only six reported decrease or no change among arctic foxes. Five of these covered a belt north and south of the boundary between Manitoba and the Northwest Territories (from Eskimo Point, no change was reported to the south and increase to the north-west) and the other was in the north-west of Victoria Island. In groups 5, 6 and 7 this was the second year in which little but increase was recorded; but in groups 8 and 9 and at Chesterfield Inlet and Baker Lake (group 4) these were almost the first signs of recovery.

The increase apparent as far west as the east part of group 9 does not seem to have occurred at Bathurst Inlet or inland to the south and west. Along the coast west of the Coppermine River and east of Richards Island there seems to have been some improvement on the previous year although there is some conflicting evidence about this.

Snowy owl. Two changes in the trend of snowy owl populations are indicated: (1) increase throughout group 1 and west to Leaf River; (2) partial decrease in Baffin Island where nothing but increase was observed in 1936–37. Elsewhere, except that there were fewer reports of increase in groups 3 and 4, it is hard to get any clear picture of what was happening. It can only be noted that in groups 8 and 11 half the 12 observers stated that increase had occurred; compared with one-third the previous year.

In certain winters abnormally large numbers of snowy owls are observed far south of their normal range, and it is believed that these southern flights are connected with the failure of the owls' food supply in the north. In view of the importance of testing this belief by correlating the southern flights with the date of the present enquiry, Mr Charles Elton suggested that a special enquiry should be made in the southern parts of Canada. This seemed particularly desirable since some other reports received indicated that snowy owls had appeared in some places in south-eastern Canada in greater numbers than usual during the early winter of 1938–39. The National Parks Bureau arranged to send out a questionnaire and obtained some useful facts. It is not proposed, however, to discuss them here because they can best be treated in connexion with the next year's report, and because the whole matter of the southern flights of the snowy owl is now being studied by a group of Canadian and American biologists who will be able to conduct a wider and more thorough survey, and with whom the Bureau of Animal Population will co-operate closely.

Sledge dog. The general situation is fairly clear from Table 3 and Fig. 2: an epidemic down the lower Mackenzie River valley, a few outbreaks of disease widely scattered across the continent, and otherwise nothing serious.

Table 3. *Information about sledge dogs*, 1937–38

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

(*a*) *Disease or epidemic reported.* (More serious outbreaks indicated +.)

Quebec and Labrador.

\+ *Natashquan.* "Quite a few dogs died in the early part of the winter. Sickness same as in previous outfit—unknown."

\+ *Senneterre.* "Disease prevalent amongst sledge dogs during summer and fall months. Symptoms: swelling of joints and running matter from the nose."

\+ *La Sarre.* "Sledge dogs kept from 50 to 100 miles north of here were affected by disease during July and August 1937, many died. Symptoms were swelling of the throat and the joints of the legs, with running matter from the nose. These symptoms usually developed about three weeks before death. Sledge dogs kept about 30 miles north of the post developed and died of this disease during the period Sept.–Dec. 1937." (2+)

Port Burwell. "Disease in Feb. and Mar. Only symptoms were lack of energy and no desire to eat."

\+ *Great Whale River.* "Sickness practically all winter. Quite a number have died."

Ontario.

\+ *Ombabika.* "Nearly all the Indian dogs had some kind of disease, got thin and died last summer."

\+ *Fort Hope.* "An epidemic occurred among sledge dogs last fall killing most of them."

Bearskin Lake. "Sledge dogs were subject to epidemic last winter (local, not general). During the coldest weather a few of the dogs got sick: went off their feed, coats got very shaggy. No other symptoms."

Manitoba.

\+ *Island Lake.* "Several sledge dogs took sick during the winter and all efforts failed to fatten them up. Several died during the break-up period in a very bloated condition."

\+ *Shamattawa.* "Distemper spread amongst the sledge dogs at the beginning of the warm weather in May 1937. Lasted all summer until fall 1937. 50% died."

\+ *York Factory.* "June–Aug. several sledge dogs died with a disease having the following symptoms: running discharge from eyes and nose, sneezing and staggering."

Saskatchewan.

\+ *Clear Lake.* "Dysenteric epidemic among dogs in August 1937. 60% animals affected with 50% mortality."

Fond du Lac. "Mild epidemic of distemper during the winter, but fully recovered in the early spring. Very few deaths reported."

10. *Lake Athabasca.* "Distemper quite common...striking at intervals."

British Columbia.

\+ *Nelson Forks.* "There appeared to be a disease among sledge dogs this winter and several had to be destroyed. The animals first would not eat, grew thin and weak, and what appeared to be a kind of paralysis set in."

Northwest Territories.

1. Baffin Island

32. *Lake Harbour.* "Two pups died."

Clyde River. "Sickness in middle of winter. Vomiting gall: perhaps undernourished."

2. Great Slave Lake Region

\+ *Rocher River.* "Distemper in Jan. and Feb. Quite a number died."

Fort Reliance. "Excess salivation, running eyes, 'hysteria', paralysis (in order given) was going on in the R.C.M.P. teams at Reliance 18–19 June, 1937. No deaths up till then." (Report No. 31 of 1936–37 enquiry.)

5. *Fort Reliance.* "Running about, yelping and frothing at the mouth, in June."

\+ *Fort Providence.* "Six dogs died this spring of distemper, mostly pups. All dogs in bush reported O.K."

Table 3 (*continued*)

\+ **11.** *Fort Providence.* "Distemper was first noticed in the Tathlina Lake area in latter March and eventually broke out in this settlement."

Hay River. "No noticeable disease among dogs but about 3 or 4% suffered from paralysis in lower back and hind quarters during Nov. and Dec. About 20% of these died: all old dogs."

3. Mackenzie River Valley

Fort Norman. "Several isolated cases of distemper. The disease appeared to come from Fort Good Hope to Burnt Lake and from there into Fort Norman. In March two pups and one dog died. Dogs became paralysed in hind quarters."

\+ **3.** "*Forts Norman* and *Good Hope* (Jan., Feb.) and *McPherson* (Apr.) had many fatal cases of distemper. Milder at *Aklavik* where a few cases occurred towards the end of May." (4 +)

\+ *Fort Good Hope.* "A lot of dogs died with distemper in the Fort and in the Indians' camps in the bush. Some Indians said that their dogs had died of some other, unknown, sickness."

\+ **26.** *Fort Good Hope.* "Animals first appeared very listless, some dry-eyed, others with heavy yellow mucus continually running from eyes. From one day to a week later dogs became partly paralysed in legs on one side of body, running into objects as if unable to see. They were taken with cramps, vomited, or tried to, became considerably weakened and died. First noticed here in the last week in Feb., continuing among most dogs, some of which recovered. Numbers lost: R.C. Mission, three out of six; R.C.M.P., five out of eight; Indians, nine out of about 30. The middle of March it was reported among the dogs at the headwaters of Ramparts River where some 60 dogs died out of 180. The end of March a few cases were reported at Coville Lake and Lac des Bois. There are about 100 dogs in that district and about six died out of twelve affected." (3 +)

\+ **24.** *Fort Good Hope.* "Distemper. Nov.–Feb. Dogs refuse food and die in a week."

\+ *Arctic Red River.* "Quite a lot of dogs died from distemper during winter and spring."

\+ *Fort McPherson.* "A severe epidemic of distemper occurred among sledge dogs in this region immediately after Indians had made a trip to Fort Dawson in the Yukon. Many dogs succumbed quickly."

\+ *Aklavik.* "Disease prevalent during spring months. Symptoms: running at nostrils and eyes, refuse food. No signs of madness. White trappers and natives both losing dogs."

\+ **17.** *Aklavik to coast.* "Discharge of matter from eyes and nose. Paralysis of hind-quarters, obvious congestion of lungs and in some cases blindness. Occurred in late April and May. The epidemic was evidently distemper and from reports travelled down the river from Fort Good Hope, attacking dogs at Arctic Red River and Fort McPherson, being carried from post to post by visiting dog teams. This disease was not the so-called 'crazy disease': none of the dogs ran about or foamed at the mouth. The R.C.M.P. at Aklavik lost 13 dogs. The disease appeared to take greater toll of the younger dogs, although some of the old dogs died from it. Other dogs died in the settlement, but some groups took only a very mild form of it and recovered."

\+ **14.** *Mackenzie River Delta.* "Dogs lost appetite and died sometimes within a week; in some cases with a froth round the eyes and mouth. Some recovered. Started about Christmas and still continues (15 June). May have been some form of distemper, probably brought by Indians from Dawson."

(*b*) *Disease reported absent* (see also Table 1)

Quebec. Seven Islands. Bersimis. Weymontachingue. Oskelaneo. Woswonby. Chibougamau. Mistassinny. **Ontario.** Missanabie. Mattice. Grassy Narrows ("*very few dogs*"). Moose Factory. Windigo. Deer Lake. Trout Lake. **Manitoba.** Rossville. Norway House. God's Lake. Cross Lake. Wabowden. Gisipigimack. Pukatawagan. Granville Lake. South Indian Lake. **Saskatchewan.** Pelican Narrows. Lac la Ronge. Stanley. Souris River. Pine River. Buffalo River. South Reindeer Lake. **Alberta.** Fort McKay. Fort Chipewyan. Hay Lakes. Upper Hay River. Fort Fitzgerald. **British Columbia.** Fort St James. Tacla. Fort Nelson. **N.W. Territories. 27.** Southampton Island. Fort Smith. Fort Liard (also **7**). **13.** Fort Providence. [**4.** Flat River, McMillan Lake and Bennett Creek locality via Fort Simpson.] **2.** Arctic Red River to Aklavik and Fort Good Hope ("*No epidemic of disease for 15 years*"). **9.** Point Separation.

There is some disagreement among the reports about dates, about whether or not disease was present at all, and if so how serious it was. Few reports are as good as no. 26 from Fort Good Hope, which gives symptoms, dates and the number of dogs affected out of the total at risk. Without a greater amount of similarly detailed information the + symbols on the map must necessarily be of rather arbitrary significance. However, the records have shown the absence, during the three years 1935–38, of any pandemic among sledge dog teams.

The symptoms indicate that it was mainly so-called "distemper" and not "crazy disease" present in the afflicted regions. Information in the reports about diet and its possible relation to the outbreaks is being kept on file.

4. Summary

1. 105 answers were received to questionnaires on population trends during 1937–38 of lemmings (*Lemmus* and *Dicrostonyx*), arctic foxes (*Alopex lagopus*) and snowy owls (*Nyctea nyctea*) in the Canadian Arctic.

2. Lemmings, "mice", arctic foxes and snowy owls were reported on the increase up most of the Labrador coast and west to Fort Chimo.

3. At the four posts Leaf River, Payne Bay, Diana Bay and Stupart Bay foxes were scarce, at three of them snowy owls had decreased, but only at Diana Bay was there a correlation with decrease in lemmings.

4. Lemmings increased further west in Hudson Strait and south to Port Harrison. In the same area, and also south to Eastmain, there was marked increase in foxes; but not to the same extent in snowy owls.

5. There was an improvement in foxes from Baffin Island (second year of recovery) to the west coast of Victoria Island (first year of recovery) and south-east over 1000 miles to the south shore of Hudson Bay (but excluding parts of the west shore). This increase corresponded with reports of increase or abundance among lemmings in southern Baffin Island and parts both of northern Baffin Island and of Victoria Island. Elsewhere, the correlation was less general. Snowy owls showed signs of decreasing on Baffin Island, perhaps foreshadowing a decrease in lemmings, for which there was evidence in the reports.

6. West and south from Bathurst Inlet conditions had improved very little; but between the Coppermine River and the Mackenzie delta increase in all three species was more commonly reported than in the previous two years 1935–37.

7. Sledge dogs were on the whole free from epidemics but a severe outbreak of "distemper" occurred throughout the lower Mackenzie River Valley.

References

Chitty, D. & Elton, C. (1937). "Canadian Arctic Wild Life Enquiry, 1935–36." J. Anim. Ecol. 6: 368–85.

Chitty, D. (1938). "Canadian Arctic Wild Life Enquiry, 1936–37." A. Anim. Ecol. 7: 381–94.

POPULATIONS OF *THRIPS TABACI*, WITH SPECIAL REFERENCE TO VIRUS TRANSMISSION[1]

By WALTER CARTER[2]

Pineapple Experiment Station, University of Hawaii, Honolulu, Hawaii

(*With Plate* 10 *and* 4 *Figures in the Text*)

CONTENTS

		PAGE
1.	Introduction	261
2.	Methods	261
3.	*Thrips tabaci* populations and disease in *Emilia*	262
4.	Records of flight obtained from trap catches	270
5.	Incidence of yellow spot disease in pineapple plants	273
6.	Summary	276
	References	276

1. Introduction

Thrips tabaci Lind., the onion thrips, is an insect of world-wide distribution, and with an extensive host range. Within recent years it has been shown to be the vector of virus diseases (2, 4, 5) of the type that require an incubation period in the insect vector, and in which, virus, vector, and host plant comprise an inseparable ecological trinity. It was with the object of determining the seasonal fluctuation of *T. tabaci* populations, and the relationships between these and disease incidence that this study was initiated.

2. Methods

Apart from onions, one of the most widely distributed and favoured host plants is *Emilia sonchifolia* DC. This species was referred to by Linford (2) as *Emilia sagittata* (Vahl) DC. St John & Hosaka have later (3) established *Emilia sonchifolia* DC. as the correct name. It is one of the first weeds to appear following denudation from cultivation, clearing, road grading or the like. It was early shown (2) to be an important host for yellow spot virus. This host was therefore chosen as most satisfactory for the purpose of this study. Samples were taken from four places chosen primarily to represent different conditions of rainfall and to a lesser degree, temperature.

The usual method was to collect the *Emilia* plants by traversing the area

[1] Published with the approval of the Director as Technical Paper No. 107 of the Pineapple Experiment Station, University of Hawaii.

[2] The collection of data on which this paper is based has been a departmental activity. Special acknowledgements are due to Mr K. Ito who collected the samples, and Mr K. Sakimura who prepared the data from wind traps. Determination of thrips species were made by Mr Sakimura and D. Moulton.

and pulling one plant every five paces. These plants were bagged together for each area and on the following day were separated, the thrips removed by shaking onto a black cloth, the leaves carefully examined and the flowers, if any, dissected. This method involved some possibility of movement by thrips among the plants while the latter were conglomerated, but since total populations were used to obtain average populations per plant sampled, such movement, if any, would not affect the data presented. Evidence that such movement does not occur significantly, however, is available in the data of which Table 5 is the summary. Although diseased and healthy plants were mixed indiscriminately in the sample bags, the average populations on the diseased plants were higher than on the healthy plants. Averages only are shown in Table 5 but the individual data show a high degree of consistency.

The stage of growth of the host plant presented some difficulty. In view of its rapid growth, free flowering, senescence and frequent re-seeding, plants of all sizes and conditions of growth were included in a single sample. To include some measure of these differences, plants were measured as to length, and the number of flower-heads, if any, recorded. Since no relationship between detailed plant measurements and *Thrips tabaci* populations is apparent from the data, these details have been omitted from the tabulation.

With the intrusion of other plants, particularly grasses, the *Emilia* stage of succession would pass from the original location, in which case some immediately contiguous area was chosen. In the type of cultivation in practice, pineapple fields are found in any one locality in all stages from fallow, through freshly planted fields, to old fields in which cultivation has ceased. There is therefore, a situation which permits *Emilia* to flourish essentially without interruption. While the plants were being examined for thrips they were also inspected for symptoms of yellow spot and diseased plants recorded.

Data on flight of *Thrips tabaci* were obtained by means of tanglefoot screens fastened to a frame which was kept headed into the wind by means of a large rudder. Tanglefoot screens were substituted for wire screens as described by Fulton & Chamberlin (1), owing to the difficulty of recovering thrips from the collection jars used by those workers.

3. *Thrips tabaci* populations and disease in *Emilia*

Data from all four stations are presented in Tables 1–4 and in graphic form in Figs. 1–4. An aerial photograph of one station (Area 3, Kipapa) is shown on Plate 10.

Although population density varies widely between locations, the seasonal trend is similar at all four points, with populations decidedly lower in the winter months. This is true of populations per plant as well as percentage of plants infested and from these data it may be deduced that the total populations in the several areas fluctuated similarly. The lag between the curves

Table 1. *Area* 1, *Kunia, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
5 Apr.	177	13·56	0·19	11·86	
1 June	135	27·40	0·9	1·48	
3 July	227	29·95	0·67	1·32	Practically no diseased *Emilia*. Succulent young growth abundant
3 Aug.	140	17·85	0·37	2·85	
7 Sept.	160	6·87	0·10	11·87	Field becoming weedy along periphery. Luxuriant new growth of *Emilia*. Few diseased
2 Oct.	114	2·63	0·02	3·50	Luxuriant growth of *Emilia*
1 Nov.	100	12·00	0·19	1·00	*Emilia* within field area old. Field recently weeded
18 Dec.	134	10·45	0·20	2·99	Fair growth, very few diseased
1935:					
8 Jan.	129	3·88	0·05	1·55	Growth good in field area. Very few diseased plants
7 Feb.	142	2·81	0·04	1·41	Luxuriant *Emilia*, very few diseased
6 Mar.	146	6·16	0·13	9·58	Good growth of *Emilia*. (These records were taken approximately 1 week after heavy rains and floods)
4 Apr.	120	5·00	0·08	1·66	Field weedy
7 May	56	26·79	0·84	0	Field generally weeded. Very few *Emilia*. Picked all available
7 May	111	36·94	0·82	18·02	*Emilia* fairly common
13 June	99	7·07	0·13	2·02	Very few *Emilia* along periphery. Too dry. Sampling transferred to contiguous field
9 July	82	2·43	0·02	3·66	Few *Emilia*, very dry
14 Aug.	82	0	0	1·22	Very few scattered *Emilia* plants between beds. Picked all available. Practically no *Emilia* along periphery, too dry. Other weeds dried also
12 Sept.	55	0	0	5·45	Picked all available *Emilia* at not less than 5 pace intervals. Very few weeds along periphery. Horseweeds reviving after recent showers
11 Oct.	145	0·68	0·01	2·06	Fair growth of new *Emilia* seedlings
14 Nov.	228	2·63	0·03	0·88	
13 Dec.	141	9·93	0·14	0·71	Area ploughed; contiguous field sampled. *Emilia* luxuriant and fairly abundant, very few diseased
13 Dec.	235	0·43	0·004	0	*Emilia* abundant along periphery, mostly new seedlings, none diseased. Area ploughed

Table 2. *Area* 2, *Wahiawa, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
5 Apr.	95	9·47	0·42	0	*Emilia* abundant but growth coarse
1 June	75	25·33	0·42	0	
3 July	147	39·45	1·57	10·20	Spring growth of *Emilia*
3 Aug.	184	11·41	0·16	6·52	
7 Sept.	110	0·90	0·009	5·45	Recently weeded; few *Emilia* except along periphery. New growth on old stock
2 Oct.	125	6·40	0·07	8·80	New growth of *Emilia*
1 Nov.	158	13·92	0·21	0·63	
18 Dec.	124	16·13	0·25	6·45	Fair growth of *Emilia*: few diseased
1935:					
8 Jan.	146	6·16	0·10	4·79	
7 Feb.	111	10·81	0·22	1·80	Recently weeded; few *Emilia*
6 Mar.	126	19·05	0·28	6·35	Fair growth of *Emilia*: few diseased. (Notes taken about one week after heavy rains and floods)
4 Apr.	107	36·45	0·95	11·22	*Emilia* not so abundant but common enough for adequate sample
7 May	108	76·85	6·11	25·00	*Emilia* mostly healthy and young
13 June	145	38·62	1·00	17·93	Few *Emilia*; dry and recently weeded.
9 July	64	15·62	0·20	37·50	Dry and recently hoed. Very few *Emilia*—picked all available
14 Aug.	105	15·24	0·38	17·14	Picked all available *Emilia*
12 Sept.	92	6·52	0·16	6·52	Very few *Emilia*; few weeds in field
11 Oct.	109	38·53	1·05	2·75	
14 Nov.	89	10·11	0·16	6·74	
13 Dec.	140	11·43	0·16	5·00	*Emilia* abundant, luxuriant growth. Mainly new seedlings with very few diseased plants

Table 3. *Area* 3, *Kipapa, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
7 Mar.	104	56·73	1·50	28·85	Plate 10, 2 A. *Emilia* growth luxuriant. Fair number of diseased plants
5 Apr.	128	57·81	2·28	14·84	
1 June	112	72·32	3·48	32·14	
3 July	152	67·10	2·94	50·00	Diseased *Emilia* prevalent
3 Aug.	110	50·90	2·00	46·36	
7 Sept.	128	10·93	0·18	33·54	Very little new growth; plants mostly old and diseased; field weedy
2 Oct.	122	19·67	0·41	57·37	Field weedy
1 Nov.	158	5·63	0·06	6·96	Field weedy. New growth of *Emilia* shows few diseased plants
18 Dec.	131	0·76	0·01	6·87	Luxuriant new growth. Few diseased plants
1935:					
8 Jan.	117	0	0	6·84	Luxuriant new growth. Very few diseased plants
7 Feb.	133	0	0	0·75	Luxuriant *Emilia*. Field becoming very weedy
6 Mar.	152	1·32	0·01	0	Field weedy but *Emilia* plentiful and mostly healthy. (These records were taken approximately one week after heavy rains and floods)
4 Apr.	134	6·72	0·09	0	Field very weedy
7 May	57	5·26	0·07	1·75	Dry: only few old *Emilia*
13 June	137	46·72	1·34	38·69	Plate 10, 2 B. *Emilia* abundant; majority diseased, dry
9 July	190	14·73	0·24	57·89	Dry, but fair number of *Emilia* plants
14 Aug.	221	29·41	0·63	57·47	*Emilia*, mostly old stand, fairly common but rather withered. Natal and crab grasses predominant. Dry
12 Sept.	169	11·24	0·22	53·25	No new *Emilia* seedlings, all new growth on old stocks
11 Oct.	179	36·87	1·11	43·57	Area becoming too weedy with grass for healthy *Emilia* growth. *Emilia* mostly of old stock, some new seedlings
14 Nov.	118	5·08	0·09	27·11	Area ploughed up after sampling
13 Dec.	110	2·73	0·04	13·64	Plate 10, 2 C. *Emilia* seedlings still small; picked all available

Table 4. *Area 4, Waimea, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
1 June	125	51·20	1·35	53·60	
3 July	157	46·49	1·12	29·93	Field was weeded just prior to sampling date
3 Aug.	165	70·30	5·31	78·18	
7 Sept.	147	58·50	2·08	63·94	Nearly all old diseased *Emilia*. New growth scanty
2 Oct.	136	45·58	1·28	30·88	Field weeded. Very little *Emilia*. Peripheral vegetation wilting due to drought
1 Nov.	144	16·66	0·26	40·27	Very little new growth due to recent weeding
18 Dec.	164	17·07	0·27	16·46	Fair growth of *Emilia* along uncultivated edges. Field proper recently cultivated
1935:					
8 Jan.	170	27·65	0·68	42·94	Little new growth, majority of the older plants diseased
7 Feb.	139	67·62	2·97	46·04	Good growth of *Emilia*, fair amount of disease in old specimens
6 Mar.	204	44·11	1·06	24·02	Field recently weeded; few *Emilia*. (These records were taken approximately one week after heavy rains and floods)
4 Apr.	151	53·64	1·82	26·49	Few *Emilia*; field recently weeded
7 May	157	49·68	1·62	25·48	Few *Emilia*; field recently weeded
13 June	210	48·09	1·27	48·09	Field weedy with young weeds. *Emilia* fairly common, good growth, mostly diseased
9 July	166	38·55	0·74	60·84	Good growth of *Emilia*; some disease among young seedlings
14 Aug.	139	40·29	1·28	38·13	*Emilia* fairly common and in fair state of growth. Field weedy mainly with crab grass
12 Sept.	165	14·54	0·30	23·63	Crab grass predominant with horseweed interspersed. Fair *Emilia* growth, few diseased
11 Oct.	153	42·48	1·22	20·91	Field very weedy; *Emilia* fairly common in field
14 Nov.	170	35·88	1·10	37·05	
13 Dec.	154	30·52	0·51	29·22	Field very weedy with grasses and horseweed. *Emilia* luxuriant along periphery and field road as well as in the field. Mostly new growth with a fair number diseased

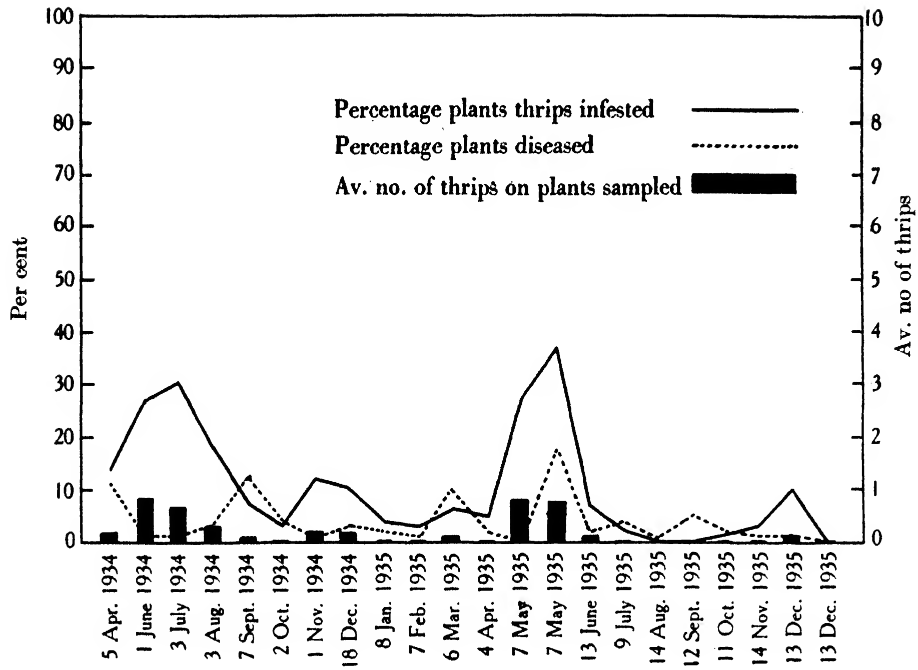


Fig. 1. Data from Area 1, Kunia, Oahu.

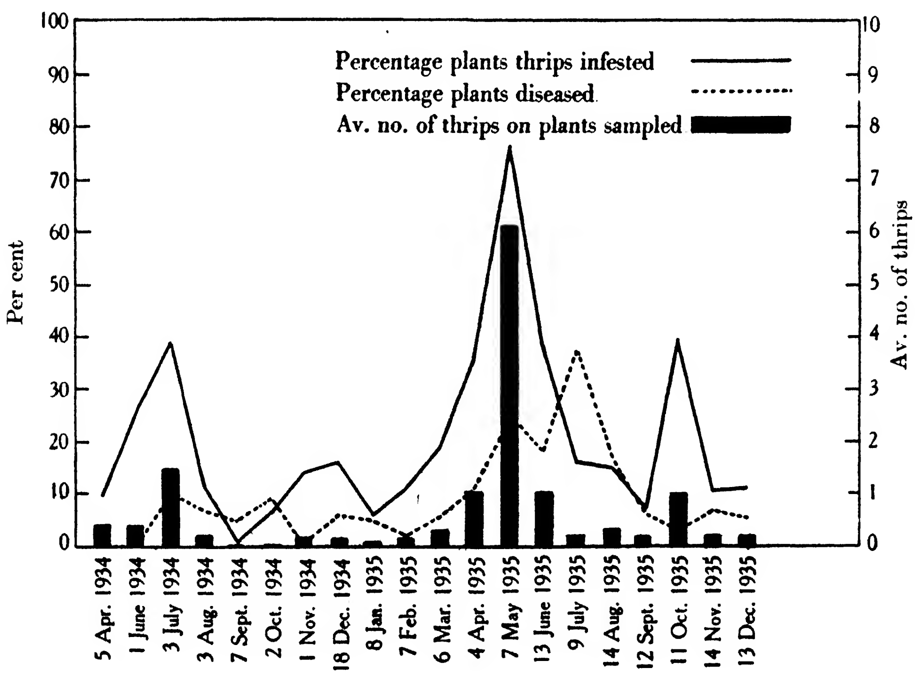


Fig. 2. Data from Area 2, Wahiawa, Oahu.

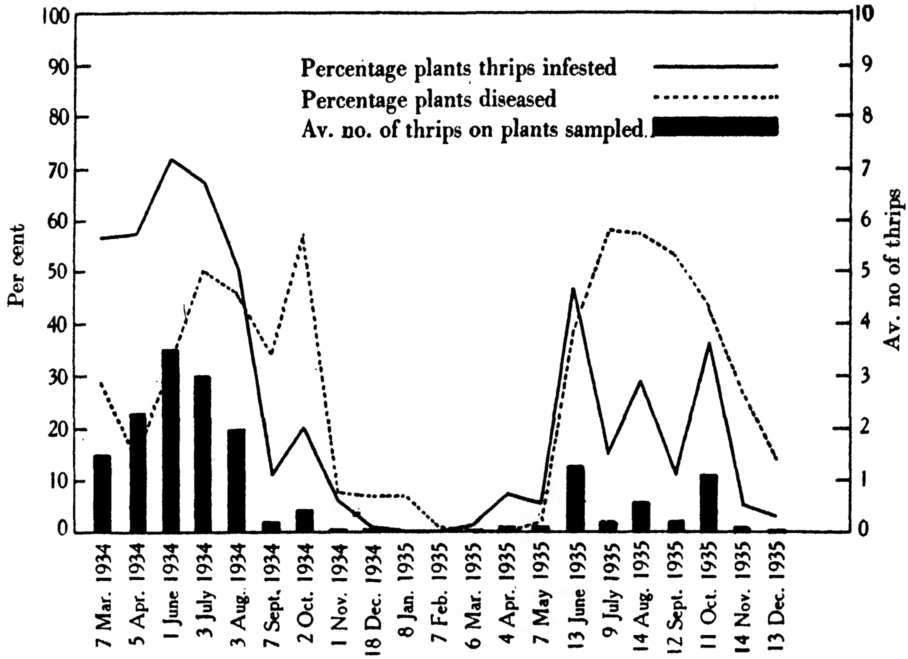


Fig. 3. Data from Area 3, Kipapa, Oahu.

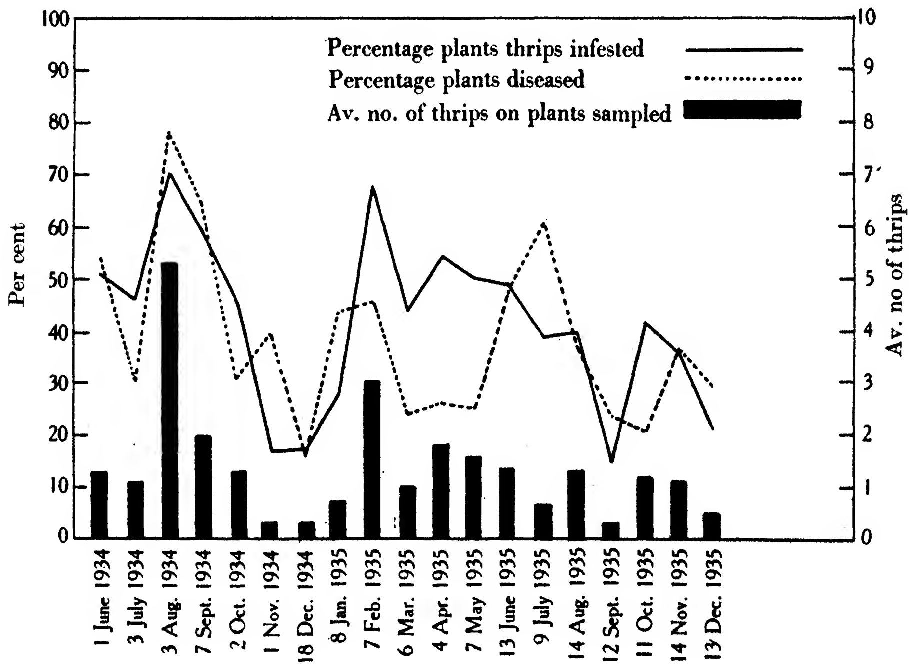


Fig. 4. Data from Area 4, Waimea, Oahu.

showing percentage of plants infested and percentage diseased is understandable when the incubation period of the disease in the plant is considered. The similarity of the two curves, however, strongly suggests that the thrips colony is sedentary and once established on an *Emilia* plant there is little movement even to other *Emilia* in the near vicinity. Any tendency on the part of *Thrips tabaci* to pass freely to and fro among *Emilia* plants would be strongly reflected in the percentage of plants diseased since only a short period of feeding by *Thrips tabaci* is necessary to infect the plant.

The only exception is seen in Fig. 3 where the divergence between the percentage of plants infested and the percentage of plants diseased in July, August and September, 1935, indicated either sudden reduction of thrips infestation by some environmental factor or the movement of viruliferous thrips from *Emilia* to *Emilia*.

Comparison of Thrips tabaci *populations on diseased and healthy* Emilia

When the plants collected from each locality are separated into the two categories of healthy and diseased and the thrips populations on the two considered, it is seen that the populations on diseased *Emilia* are consistently higher than those on healthy *Emilia*. All the data in this connexion are summarized in Table 5.

Table 5. *Summary of data from four collection areas showing relative thrips populations on diseased and healthy* Emilia sonchifolia

Collection locations, Oahu	No. of healthy plants infested	No. of *Thrips tabaci* on infested healthy plants	Average population on infested healthy plants	No. of diseased plants infested	No. of *Thrips tabaci* on infested diseased plants	Average population on infested diseased plants
Area 1, Kunia	278	598	2·2	28	55	2·0
Area 2, Wahiawa	406	1124	2·8	92	518	5·6
Area 3, Kipapa	358	1024	2·9	329	1204	3·7
Area 4, Waimea	628	1520	2·4	666	2697	4·0

The explanation for this is probably that while healthy *Emilia* normally grows rapidly, matures and dies, diseased plants may persist for a longer time with a mass of curled leaves affording satisfactory shelter for *Thrips tabaci*. It seems to be demonstrated that when *Emilia* functions as a reservoir of the yellow spot virus it is also a more suitable host for *Thrips tabaci*.

Although the collection of data from relatively restricted localities is a valid method of obtaining seasonal trends of insect populations, it cannot be presumed that such populations are homogeneous over a large area even under Hawaiian conditions, where seasonal changes are slight and violent disruption of host plant sequence rarely occurs.

Occasionally additional collections were made at points fairly contiguous to the regular collecting places and the data from these are listed in Table 6 where comparisons are possible between them and the regular collections.

It is evident that population densities are not homogeneous and "pockets" may occur wherein deviation from a standard collection point can be found.

Table 6. *Comparing data from regular collecting points with data obtained at nearby locations on same dates*

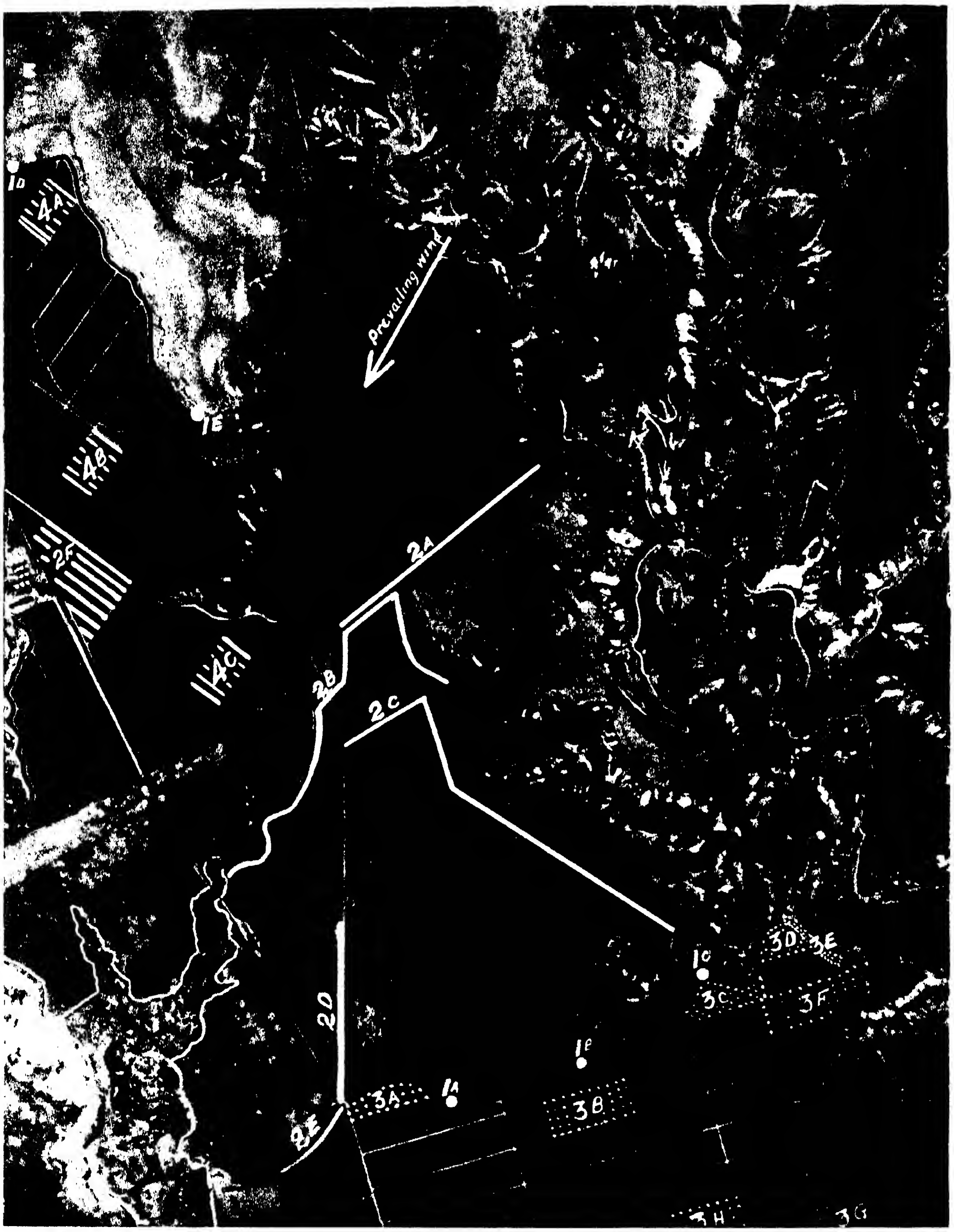
Location	No. of plants sampled	% infested	Average *Thrips tabaci* population	% diseased	Notes
Date: 7 March 1934					
Kipapa, Area 3, 2 A, Plate 10	104	56·73	1·50	28·85	Regular collecting point. *Emilia* growth luxuriant; diseased plants in fair number
Kipapa 2 D, Plate 10	66	6·06	0·08	0	Fallow field in grass: *Emilia* abundant and luxuriant
Date: 5 April 1934					
Kipapa, Area 3, 2 A, Plate 10	128	57·81	2·28	14·84	Regular collecting point. *Emilia* luxuriant: fair number of diseased plants
Kipapa 2 E, Plate 10	61	54·10	1·30	22·95	Along drainage ditch
Date: 7 May 1935					
Kipapa, Area 3, 2 A, Plate 10	57	5·26	0·07	1·75	Regular collecting point. Dry: only few old *Emilia* plants
Kipapa 2 F, Plate 10	275	90·91	10·93	60·73	No record
Date: 5 April 1934					
Wahiawa	95	9·47	0·42	0	Regular collecting point. *Emilia* abundant: growth coarse
Wahiawa A	20	30	0·3	6·7	Area recently weeded: *Emilia* scarce
Wahiawa B	54	11	0·11	0	*Emilia* abundant

4. Records of flight obtained from trap catches

Three tanglefoot traps were maintained in the area covered by systematic collections at Kipapa, Area 3 (Plate 10, 1 A, B, C). After 2 months two of the traps were removed from the original positions to the periphery of a nearby field in which detailed counts on the incidence of yellow spot in pineapples were to be taken (Plate 10, 1 D, E). Although this paper is concerned primarily with *Thrips tabaci*, all the thrips collected are listed in Tables 7 and 8, because no data on wind-borne thrips species have been published, and the comparative catches of *Thrips tabaci* and other species are significant.

It will be noted that *Thrips tabaci* occupies an extremely minor position both with respect to incidence and numbers caught. On the other hand *Taeniothrips hawaiiensis* is found almost without exception in all the collections with high populations in the winter months. *Stulothrips trespinus* shows an interesting distribution. At both places it appeared in the late August collection in small numbers. From October on to the end of the year, its incidence and numbers are both high. The large numbers at trap locations 1 D and E in October indicate a mass movement of considerable proportions. At both trap locations, the incidence of this species was high for the rest of the year.

It is interesting to note that most of the species listed attain their greatest incidence and numbers during the late fall and winter months. Several of



(*Photo by Eleventh Photo Section, A.C., Wheeler Field, T.H. Published by permission*).

Phot. 1. Aerial photograph of Area 3, Kipapa, Oahu:

1A to E—Wind traps.
2A to F—*Emilia* samples.
3A to H—Yellow spot samples.
4A to C—Yellow spot samples.

Table 7. *Area* 3 (*Plate* 10, 1 A, B, C). *Thrips caught in wind traps*

		Terebrantia, Thripidae										Tubulifera, Phloeothripidae									
Date	Trap	*Heliothrips rubrocinctus* (Giard)	*Chirothrips mexicanus* Crawford	*Taeniothrips hawaiiensis* (Morgan)	*Thrips abdominalis* Crawford	*Thrips panicus* Moulton	*Thrips saccharoni* Moulton	*Thrips tabaci* Lind.	*Isoneurothrips carteri* Moulton	*Isoneurothrips fullawayi* Moulton	*Stulothrips trespinus* Moulton	*Hoplothrips flavitibia* Moulton	*Hoplothrips paumalui* Moulton	*Aleurodothrips fasciapennis* (Frank.)	*Haplothrips fusca* Moulton	*Haplothrips gowdeyi* (Frank.)	*Haplothrips melaleuca* Bagnall	*Haplothrips (Hindsiana) sakimurai* Moulton	*Haplothrips williamsi* Moulton	*Kentronothrips hawaiiensis* Moulton	Undetermined
1935:																					
20 May	1 B	.	.	1	.	.	.	4	.	.	.	.	.	1	.	2	.	.	.	.	.
22 May	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25 May	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8 June	1 A	.	.	4	.	.	.	.	.	1	.	.	.	1	.	1	1	.	.	.	.
	1 B	.	.	4	1	.	1	1	1	.	.	.	.	.	.	2	.	.	1	.	.
	1 C	.	.	4	1	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.
13 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	1 B	.	.	4	.	.	1	.	.	.	.	.	.	.	.	1	1	.	.	1	.
	1 C	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	1	.
19 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	1	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2
	1 C	.	.	4	.	1	.	.	.	1	.	.	.	.	.	2	1	.	.	.	.
28 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.
	1 B	.	.	7	1	.	.	.	.	1	.	.	.	.	.	2	2	1	.	.	.
	1 C	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5 July	1 A	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	2	2	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	.
10 July	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
	1 B	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18 July	1 A	.	.	3	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
	1 C	.	1	2	.	.	1	.	.	.	.	.	.	.	.	3	1	.	.	1	.
24 July	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.
31 July	1 C	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
8 Aug.	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
14 Aug.	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
22 Aug.	1 C	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.
31 Aug.	1 C	.	.	2	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.
6 Sept.	1 C	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.
12 Sept.	1 C	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.
18 Sept.	1 C	.	.	4	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.	.	1
27 Sept.	1 C	.	.	3	.	1	8	.	.	.	.	.	.	.	.	1	.	.	.	6	.
4 Oct.	1 C	.	.	.	.	.	2	.	.	.	.	.	.	.	.	1	.	.	.	2	.
11 Oct.	1 C	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.
18 Oct.	1 C	.	.	5	1	.	3	.	.	.	5	.	.	.	.	.	.	2	.	.	.
25 Oct.	1 C	.	.	4	.	.	2	.	.	.	2	.	1	.	.	2	.	1	.	.	1
1 Nov.	1 C	.	.	8	.	.	.	.	.	.	.	.	1	.	1	2	.	2	.	.	.
8 Nov.	1 C	.	.	11	1	.	.	.	.	.	15	.	.	.	.	.	.	2	.	.	.
22 Nov.	1 C	.	2	19	1	.	1	.	.	.	4	.	.	.	.	.	.	1	.	1	.
29 Nov.	1 C	.	.	8	.	.	.	.	.	.	17	.	.	.	.	2	.	.	.	2	.
6 Dec.	1 C	.	.	.	2	.	.	.	.	.	4	.	.	.	.	1	.	.	.	2	.
13 Dec.	1 C	1	.	3	.	.	.	.	.	.	3	.	.	.	.	3	.	.	.	4	.
20 Dec.	1 C	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.
30 Dec.	1 C	3	1	14	3	.	3	2	.	.	2	.	.	.	.	6	.	2	.	1	.
1936:																					
3 Jan.	1 C	.	2	1	.	1	.	.	.	.	2	.	.	.	.	1	.	.	.	.	.

Table 8. *Area* 3 (*Plate* 10, 1 D, E). *Thrips caught in wind traps*

Date	Trap	Terebrantia, Thripidae: *Heliothrips haemorrhoidalis* Bouché	*Heliothrips rubrocinctus* (Giard)	*Chirothrips fulvus* Moulton	*Chirothrips mexicanus* Crawford	*Chirothrips sacchari* Moulton	*Taeniothrips hawaiiensis* (Morgan)	*Thrips abdominalis* Crawford	*Thrips panicus* Moulton	*Thrips saccharoni* Moulton	*Thrips tabaci* Lind.	*Isoneurothrips antennatus* Moulton	*Isoneurothrips fasciatus* Moulton	*Stulothrips trespinus* Moulton	Tubulifera, Phloeothripidae: *Hoplothrips paumalui* Moulton	*Haplothrips gowdeyi* (Frank.)	*Haplothrips melaleuca* Bagnall	*Haplothrips* (*Hindsiana*) *sakimurai* Moulton	*Haplothrips* sp.*	*Kentronothrips hawaiiensis* Moulton
1935:																				
24 July	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
31 July	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
8 Aug.	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.
14 Aug.	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
22 Aug.	1 D	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
31 Aug.	1 D	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
	1 E	.	.	.	1	.	1	.	.	.	.	.	.	4	.	.	1	.	.	.
6 Sept.	1 D	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	1	.	.
	1 E	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.
12 Sept.	1 D	.	.	.	.	.	7	.	3	1	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	.	.	4	.	.	1	.	.	.	.	.	.	.	.	.	.
18 Sept.	1 D	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	1	.	.	.
27 Sept.	1 D	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	1	.	2
	1 E	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
4 Oct.	1 D	.	.	.	.	1	1	.	.	1	.	.	.	.	1	1	.	2	.	3
	1 E	.	.	.	.	1	1	.	.	3	.	.	.	.	.	1	1	.	.	.
11 Oct.	1 D	.	.	.	.	.	1	.	.	.	.	.	.	1	.	1	.	.	.	.
	1 E	.	.	.	.	.	1	.	1	.	.	.	.	2	.	.	1	1	.	3
18 Oct.	1 D	.	.	.	.	.	8	2	.	2	.	.	.	32	.	2	.	1	.	.
	1 E	.	.	1	.	.	5	1	.	1	.	.	1	16	.	.	1	3	.	1
25 Oct.	1 D	.	.	.	.	.	26	4	.	.	.	.	.	20	.	5	.	3	.	2
	1 E	.	.	.	.	.	8	.	.	1	.	.	.	11	.	2	.	1	.	.
1 Nov.	1 D	.	.	.	.	.	15	1	.	1	.	.	.	.	.	3	.	2	.	.
	1 E	.	.	1	.	.	28	6	.	1	.	.	.	.	.	3	.	2	.	3
8 Nov.	1 D	.	.	1	.	.	11	.	.	1	.	.	.	.	.	2	.	1	.	1
	1 E	.	.	.	.	.	15	.	.	2	.	.	.	.	.	.	.	3	.	1
22 Nov.	1 D	.	.	.	1	.	28	11	2	2	.	.	.	7	.	5	.	1	.	2
	1 E	1	.	1	2	.	37	16	.	2	.	.	.	8	.	6	.	5	.	1
29 Nov.	1 D	.	.	.	1	.	9	5	.	2	.	.	.	13	.	2	.	.	.	.
	1 E	.	.	.	.	.	6	.	.	.	.	.	.	8	.	2	.	3	.	1
6 Dec.	1 D	.	.	.	.	.	4	1	.	.	.	.	.	2	.	.	.	.	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
13 Dec.	1 D	.	1	.	.	.	4	1	.	.	.	.	.	6	.	2	.	1	.	1
	1 E	.	.	.	.	.	2	.	.	.	1	.	.	3	.	.	.	2	.	.
20 Dec.	1 D	.	.	.	.	.	.	1	1	.	1	1	.	7	.	1	.	.	.	.
	1 E	.	.	.	.	.	2	.	.	.	.	.	.	6	.	.	.	1	.	.
30 Dec.	1 D	.	.	.	2	.	14	2	.	1	.	.	.	.	.	6	.	.	.	4
	1 E	.	1	.	.	.	11	3	3	1	.	.	.	1	.	7	.	1	.	5
1936:																				
3 Jan.	1 D	.	.	.	.	.	2	.	.	.	.	.	.	.	.	2	.	.	.	1
	1 E	.	.	.	.	.	2	.	.	1	.	.	.	.	.	1	.	.	.	.

* Further identification was impossible because of imperfect specimen.

these species occur with such regularity and in such numbers as to prove that thrips as a group are not similar to *Thrips tabaci* in habit and that many species fly freely and disperse in great numbers in wind currents. In the writer's view, the wind trap data indicate that *Thrips tabaci* is not normally a migratory species and that only a drastic interruption of its host plants over a considerable area would force a mass movement of the species. The occasional high incidence of yellow spot in localized areas in pineapple plantings is adequate evidence that movements of considerable proportions do sometimes take place.

5. INCIDENCE OF YELLOW SPOT DISEASE IN PINEAPPLE PLANTS

These data were taken from two pineapple fields in places contiguous to Area 3 (Plate 10, 3 and 4), and it was on the windward margins of these pineapple fields that the wind traps already referred to were placed.

Field 1 (Plate 10, 3). In this field, the incidence of yellow spot was observed during both susceptible periods, namely, when the plants were small, and later, during the development of the fruit. In the first-named period, yellow spot was apparently confined to a small area near the field border (Plate 10, 3 D, E). In this area, counts of infested plants in the border showed a percentage infection of 7·12. Immediately to leeward the percentage dropped to 3·54 while further in the field infection was incidental. A count made in the border area contiguous to that already mentioned showed a percentage infection of 1·57. Disease in fruit is shown in Table 9. These counts covered an area of ten field blocks of which eight are shown in Plate 10. From the table it is seen that incidence of yellow spot was extremely low.

Field 2 (Plate 10, 4). This area was abnormal in that it fruited out of season; but for the purposes of this paper this was desirable, since it provided a susceptible period during the winter months at a time when field populations of thrips were low in that area.

During November, when fruit began to ripen, preliminary counts were made, 12 November 1935, in the three blocks (Plate 10, 4 A, B, C). Two cases were observed in block 4 A out of 5400 fruits counted, none in block 4 B out of 3600 counted, and five from block 4 C out of 3000 counted. Block 4 C was fruiting more freely than either of the others and on 19 November counts in this block showed eight infected cases out of 1041 ripe fruits examined and twelve out of 4200 green fruits. From that time on regular counts were made and these are shown in Table 10.

Although the percentage of infected plants was small, there was a significantly higher incidence in block 4 C. This is believed to be associated with the discing down of the old field 2 A which lies directly to windward of the area in block 4 C from which the counts were made. This may well be an example of the postulate made previously in this paper, namely, that drastic

Table 9. *Area* 3, *Kipapa, Oahu* (*Plate* 10, 3). *Incidence of yellow spot disease in fruit crowns*

A, Number of pineapple crowns examined;
B, Number diseased;
C, Percentage diseased as determined on the following dates:

	20 May 1935			5 June 1935			13 June 1935		
Block	A	B	C	A	B	C	A	B	C
3 A	1521	5	0·33				1503	7	0·47
3 B	2044	0	0	4050	5	0·12	4045	9	0·22
3 C	753	0	0	1824	1	0·05	1823	1	0·05
3 D	917	0	0	1807	0	0	1807	1	0·06
3 E	1467	4	0·27	2886	13	0·45	2873	16	0·56
3 F							2919	5	0·17
3 G							2215	0	0
3 H							3688	6	0·16
3 I*				2767	0	0	2767	1	0·04
3 J*				4071	1	0·02	4070	2	0·05
Total	6702	9	0·13	17405	20	0·11	27710	48	0·17

	1 July 1935			15 July 1935			29 July 1935		
Block	A	B	C	A	B	C	A	B	C
3 A	1449	2	0·14	1098	3	0·27	318	4	1·26
3 B	3999	1	0·03	3194	2	0·06	654	1	0·15
3 C	1805	5	0·28	1444	2	0·14	362	1	0·28
3 D	1804	6	0·33	1698	8	0·47	973	0	0
3 E	2773	12	0·43	2241	11	0·49	1352	3	0·22
3 F	2876	5	0·17	1891	5	0·26	708	1	0·14
3 G	2211	2	0·09	1953	2	0·10	781	0	0
3 H	3682	3	0·08	3300	2	0·06	1343	0	0
3 I*	2764	1	0·04	2256	0	0	1144	0	0
3 J*	4068	0	0	3933	0	0	1828	2	0·11
Total	27431	37	0·13	23008	35	0·15	9463	12	0·13

* Not shown in Plate 10.

Table 10. *Area* 3 (*Plate* 10, 4 A, B, C). *Yellow spot disease in crowns and fruits*

	Block 4 A			Block 4 B			Block 4 C		
		Diseased			Diseased			Diseased	
Date	Normal	Crown	Fruit	Normal	Crown	Fruit	Normal	Crown	Fruit
1935:									
2 Dec.							39	1	0
8 Dec.							57	41	2
23 Dec.	73	0	0	177	0	0	128	1	0
30 Dec.	115	0	0	250	0	1	221	4	12
1936:									
6 Jan.	241	0	0	1157	1	0	1576	7	23
9 Jan.							919	5	7
13 Jan.	563	0	0	1180	1	1	2313	12	11
Total	992	0	0	2764	2	2	5253	71	55

disturbance of the host plant areas are necessary before incidence of infection assumes economic proportions.

Before yellow spot became evident in the developing crowns and fruit it was observed that scattered *Emilia* plants growing between the pineapple rows were showing a high percentage of infection. Counts made on this and later dates are shown in Table 11.

Table 11. *Records from Area* 3 (*Plate* 10, 4 A, B, C). *Thrips infestation and disease in* Emilia *growing among pineapple plants*

Date 1935	No. of plants sampled	% plants infested	% plants diseased	Av. no. of thrips per plant	Notes
8 Oct.	15	100	86·66	4·06	Scattered well-developed plants growing among pineapples, Plate 10, 4 C
30 Oct.	84	11·90	33·33	0·15	Young plants among pineapple, Plate 10, 4 B
27 Nov.	143	2·79	2·09	0·03	Plate 10, 4 A
	311	14·79	15·43	0·22	Plate 10, 4 B
	114	9·64	16·66	0·11	Plate 10, 4 C

It is evident from these data as well as from general field observations that a considerable reservoir of virus may exist in the pineapple fields with little or no transfer to pineapple plants taking place. This is readily explainable on the difference in suitability of the two plants as thrips hosts. A few scattered wind-blown thrips would be sufficient to infest and infect the relatively small populations of *Emilia* present. Infestation of pineapple plants, however, does not occur except rarely and even then only for a short period during blossoming, the thrips' sojourn on pineapple being transient. This transient stay is sufficient to infect the pineapple if the insect is viruliferous and the plant susceptible. There is no evidence to indicate movement of thrips from pineapple to pineapple, nor is movement from undisturbed *Emilia* growing among pineapple to nearby pineapple plants likely. There is, furthermore, no correlation between *Thrips tabaci* populations on *Emilia* in the sampled areas and disease in nearby pineapple fields, probably for the same reason, that undisturbed *Emilia* is a favoured host from which movement does not normally occur.

Quantitative data of the kind presented in this paper measure population per unit but not the total number of units. Under conditions normally prevailing in Hawaii the number of units in any locality contiguous to pineapple fields is high and the average population per unit host plant seems to provide a fair index, therefore, of the status of *Thrips tabaci* populations on *Emilia* in any particular locality.

Incidence of yellow spot disease in pineapple plantings is evidently conditioned by a number of interrelated factors. The higher the population of *Thrips tabaci* per unit of *Emilia*, the higher the potential incidence, but the factors governing dispersal must be operating positively and the pineapple plants be susceptible at one and the same time if incidence of the disease in

pineapple plants is to assume economic proportions. It is conceivable, however, that a large total population of thrips might disperse from an area showing a low population per unit but a large number of units, if the area as a whole was disturbed. The introduction of a new factor into the complex, such as, for example, a thrips parasite, could only be expected to influence the single factor of unit population.

6. Summary

1. Populations of *Thrips tabaci* Lind. on *Emilia sonchifolia* DC. were recorded from four locations, and data on wind dispersal of thrips species in pineapple were recorded from one location on the Island of Oahu, Territory of Hawaii.

2. Population densities varied widely between locations but seasonal trends were the same at all four points with populations decidedly lower in the winter months. The percentage of disease in *Emilia* followed closely the percentage of plants that were thrips infested, indicating that once a colony of *Thrips tabaci* is established on *Emilia* there is little movement therefrom.

3. Diseased *Emilia* plants maintain higher populations of *Thrips tabaci* on the average than do healthy *Emilia*.

4. Wind trap data indicate that *Thrips tabaci* is not a migratory species. Most of the species caught attained their greatest incidence and numbers during the fall and winter months. Incidence of yellow spot disease in pineapple is not correlated with *Thrips tabaci* populations on *Emilia* in nearby areas. This is accounted for on the grounds that *Emilia* is a favoured host from which dispersal does not normally occur.

5. Cultivation of host plant areas and drought are two possible dispersal factors.

References

1 **Fulton, F. A. & Chamberlin, J. C. (1931).** "A new automatic insect trap for the study of insect dispersion and flight associations." J. Econ. Ent. 24: 757–61.

2. **Linford, M. B. (1932).** "Transmission of the pineapple yellow-spot virus by *Thrips tabaci*." Phytopathology, 22: 301–24.

3. **St John, H. & Hosaka, E. Y. (1932).** "Weeds of the pineapple fields of the Hawaiian Islands." Univ. Hawaii Res. Publ. No. 6: 1–196.

4. **Samuel, G. & Bald, J. G. (1931).** "*Thrips tabaci* as a vector of plant virus disease." Nature, Lond., 128: 494.

5. **Smith, K. M. (1931).** "Virus diseases of plants and their relationship with insect vectors." Biol. Rev. 6: 302–44.

FURTHER CHANGES IN THE BRECKLAND AVIFAUNA CAUSED BY AFFORESTATION

By DAVID LACK

CONTENTS

		PAGE
1.	Introduction	277
2.	Description of the areas	277
3.	Methods	278
4.	The breeding birds	278
5.	Winter distributions	280
6.	Late summer distributions	281
7.	Birds of the rides	281
8.	Comparison with other areas	281
9.	Factors influencing distribution	282
10.	Summary	284
	References	284
	Appendix 1. Species omitted from Table 1 of breeding bird populations	284
	Appendix 2. Species omitted from Table 2 of winter bird populations	285

1. Introduction

In a previous paper (Lack, 1933) the changes in bird life resulting from the planting of the Breckland heaths with pine (mostly *Pinus sylvestris*) were described up to the eleventh year after planting. A further visit to the area from 10 to 20 June 1937, has extended the study to the fifteenth year after planting, while many more figures have been obtained for younger plantations. In addition, visits have been made in mid-winter and early August, in order to study the populations outside the breeding season. The present paper may also be regarded as an addition to the general paper on British woodland birds by Lack & Venables (1939), in which the influence of the height of trees could not be specially investigated. As in the case of the previous investigation, I am deeply indebted to the Forestry Commission (England and Wales) for permission to work in the Breckland forests.

2. Description of the areas

A brief description of the areas studied was given in the earlier paper; see also Watt (1937) for a recent description of the heathland vegetation. All that need be added here is that, after the eleventh year, where the young pines average some 12 to 14 ft. high, growth continues rapidly and steadily, so that the 15-year-old plantations average some 23 ft. high. About the thirteenth year, but varying locally, the Forestry Commission cut away the lowest branches of the trees, and from now on the trees begin to be thinned out.

The removal of the lower branches affects adversely some of the species typical of secondary growth. Cones first appear in 7- or 8-year-old trees, and are common in 14- andl 5-year-old plantations. This affects the crossbill, which has occurred outside the breeding season in a 14-year-old plantation.

3. Methods

The observer walked through the various plantations noting every individual of every species seen or heard; especially in the denser plantations, the ear was more valuable than the eye. For comparing the populations in the different types of plantations, the total number of individuals of each species in each type of plantation was calculated as a percentage of the total number of individuals of all species in that type of plantation. (Therefore the figures are only comparative, but this is all that is needed for demonstrating the changes in species composition. Complete censuses are quite impracticable in the denser plantations.) For example, in 10-year-old plantations 197 birds were counted, of which 77 were willow warblers, giving a figure of 39%. Table 1 gives the species composition of each type of plantation in the breeding season calculated in this way. At the foot of the table is also given the total number of individual birds counted; 4-, 12- and 15-year-old plantations are represented by smaller totals than the others, hence the percentages for these may be rather less reliable.

It was not thought necessary to publish the actual counts, since these can be assessed from the percentage figures and the total of all individuals counted. Nor was it thought necessary to give precise localities. All refer to well-grown plantations near Thetford, Brandon or Harling, close to the Norfolk-Suffolk border. Some Breckland plantations have grown exceptionally poorly. Some of these counts were given in the earlier paper, but such areas were not included in the present investigation, except that the 12-year-old plantation was unavoidably poor—no better one was available. Full counts and precise localities, which are of interest only to someone working in the district, are being deposited with the British Trust for Ornithology, at Oxford.

Table 1 gives a full list of the breeding species met in the plantations during the counts except for a few listed in Appendix 1. Game birds and birds of prey, which have been greatly influenced locally by man, and a few other species of uncertain distribution, were omitted. Appendix 2 gives a similar list of species omitted in making Table 2.

4. The breeding birds

These are summarized in Table 1. On the "brecks", which have close-cropped grass, many bare and stony areas and rabbit burrows, seven species breed. Wheatear and stock dove nest down rabbit holes, stone curlew, lapwing,

skylark, red-legged partridge and locally the ringed plover, nest on the bare ground. Preparatory to planting with pines, rabbits are cleared and the burrows are filled in, while the grass grows taller. The bird population of such areas is not dissimilar to that of the natural heaths of the area, on which planting also occurs. On the heaths, which contain a variable proportion of *Calluna*, grasses (*Agrostis, Festuca*) and bracken (*Pteridium*), most of the bare "breck" species (wheatear, stock dove, stone curlew, lapwing, ringed plover) are very local. The skylark remains common, the meadow pipit is also common; and common partridge and, locally, yellow wagtail, also appear. Where the heath vegetation is taller, stonechat and whinchat colonize. These two vary similarly with regard to height of vegetation, but the former is mainly on *Calluna* and the latter mainly on grass heath. This difference accounts for their rather erratic distributions in Table 1.

The bird population of well-grown heaths is unaffected by pine plantations under four years old. After this, skylark and meadow pipit decrease rapidly, disappearing about the ninth year. Stonechat and whinchat, which are "scrub" species, increase in the fourth and fifth year, but then decrease. The willow warbler first appears in the fourth year, rapidly increases, and is the commonest species from the seventh to twelfth year, after which it declines in importance. Whitethroat and wren, which are occasional in tall, thick, heathland, become moderately common from the fifth to the twelfth year, but decrease when the lower branches of the pines are cut. The dunnock, another species characteristic of the secondary growth of woods, shows a very similar distribution, but first colonizes rather later.

Blackbird and song thrush colonize in the sixth and seventh years respectively. The latter is only local, but the former is characteristic of older plantations, and seems to be still increasing. The chaffinch, which first appears in the seventh year, becomes the commonest species in the fourteenth and fifteenth years. (It is the commonest bird in mature pine woods.) Two other characteristic pine wood birds, coal tit and goldcrest, colonize about the same time as the chaffinch, and are gradually increasing. The robin may also be increasing, but is as yet local. Finally, the ring dove has colonized the 14- and 15-year-old plantations.

In addition to these, various other species have bred occasionally (see Table 1). Of special interest are tree pipit and wood lark, which are driven from the heaths and brecks by the plantations, but return in the fourteenth or fifteenth year. Their typical habitat is heathland with a few tall trees. They disappear when the heathland is replaced by young pines, even when a few tall trees have been left, but return when the young plantations are tall enough to act as song posts, and nest in the heath vegetation provided by the rides and forest edges. One other species driven out by the planting will also return, but not till considerably later. The stock dove breeds in holes in rabbit burrows on the brecks and also in old trees.

Lack & Venables (1939) describe the avifauna of older pine plantations. From comparison with this it can be seen that by the fifteenth year a number of species characteristic of older plantations have still not colonized, especially such as the tree creeper and various tits and woodpeckers, which require holes or ledges in old trees for nesting, and such as various birds of prey, which nest high in the trees. Most other pinewood species found in eastern England have now colonized.

The rapidity and steadiness of the changes in the avifauna, correlated almost entirely with increasing height of the trees, are remarkable, and provide an almost unique example of an ornithological succession. Since huge areas of the Breckland have now been planted, one wonders where this enormous number of colonizing birds has come from, and where the dispossessed heathland birds have moved to.

5. Winter distributions

Counts were taken between 26 and 29 December 1936, and between 15 and 19 December 1937. Owing to the smaller totals involved, the results of Table 2 are calculated for 2-year groups. The total density of the bird populations in the plantations is considerably lower in winter than summer. Some species, such as the tits and goldcrest, tend to collect in foraging parties, and the occurrence of such large, but irregularly distributed, parties makes the figures less uniform than in the breeding season.

In the winter, summer visitors to England, such as the warblers and the whinchat, are of course absent. Skylark, meadow pipit and stonechat frequent the same habitats as in the breeding season but leave the plantations at a younger age, while the stonechat also spreads on to low heathland. The wren is more abundant, and spreads on to the heaths, where it does not breed. Dunnock, robin and blackbird remain about the same save that the blackbird also feeds on the heaths, where it does not nest. Goldcrest, coal and blue tits show a marked increase, especially the two tits, and occur in rather younger plantations than in the summer. The chaffinch and ring dove leave the plantations completely. Jay, tree creeper and crossbill, three birds which breed only in plantations rather older than those yet found in the Breckland forest, occur in the older plantations out of the breeding season. A few other species occur occasionally, as can be seen from Table 2.

No winter counts were taken on the bare brecks, which have a small population rather similar to that of cultivated land, with flocks of lapwing, starling and various Turdidae. The green woodpecker also feeds here, and on the heaths, but never far from trees, to which it retires if disturbed.

Table 2 shows that there is a succession of different species in winter as there is in summer, but fewer species are involved, so the results are less striking.

6. Late summer distributions

Counts were also taken between 9 and 12 August 1938. The data were not sufficient for percentage tabulations, so the actual counts are given in Table 3. By this date some species have already taken up their winter distributions. Thus all save one chaffinch had already left the plantations, the coal tit, blue tit and goldcrest were already in large foraging parties and were spreading into younger plantations. These foraging parties were also joined by willow warblers, many of which had not yet departed, and an occasional dunnock, whitethroat, robin, chaffinch, and other tits. No other points need special comment. A few species were recorded occasionally which have not been recorded at the other seasons (see Appendix 1).

(Small parties up to eight chaffinches, and larger flocks of tree sparrows, were seen in certain 5- and 6-year-old plantations in late June 1937. These birds were definitely not breeding there, but had moved in from elsewhere; all save an occasional tree sparrow had left by early August.)

7. Birds of the rides

Wide rides have been left in most plantations. These usually possess a typical heathland vegetation, and are frequented in small numbers by typical heathland birds, notably skylark, meadow pipit, stonechat, stone curlew, common and red-legged partridges, while various Turdidae and the green woodpecker feed there. The occurrence of tree pipit and wood lark has also been mentioned. Save for the two last, which depend also on the adjoining plantations, the birds of the rides were omitted from the counts of the plantations.

8. Comparison with other areas

Schiermann (1934) has made a comparable study of the breeding birds of the pine plantations in North Germany, in less detail for the younger plantations, but including more data from older plantations than those yet found on the Breck, and he has also worked out total densities. Schiermann's data show that the growth of the pines in his area is closely similar to that on the Breck, and a comparison of the birds which breed in both areas shows that their distributions with regard to height of trees are extremely similar in most cases. The similar distributions do not require comment, but two species are strikingly different. The chaffinch colonizes the Breckland plantations in the ninth year, the North German plantations not until the twentieth year; and the coal tit colonizes the Breckland plantations in the eleventh year, the North German plantations not until the thirty-fifth year. Possibly the German coal tits nest only in holes in trees and not also in holes in the ground as British coal tits do, for this latter habit alone makes possible the colonization of such young plantations.[1] The chaffinch uses trees for song posts and for

[1] This seems more likely to be due to an absence of holes in the ground in the German plantations than to a difference in the habits of the birds.

nesting, but it is quite unknown why the German birds should need so much higher trees for this purpose than the Breckland birds.

It had been hoped to compare the Breckland populations with other afforested areas in Britain, but none of those so far visited have proved suitable. Usually the plantations are not sufficiently extensive to get large enough counts, and in many cases the growth of the trees has been far less uniform than on the Breckland, which seems to offer specially favourable conditions. In the extensive plantations on the Culbin sands, Moray Firth, Scotland, the trees have grown much less regularly, and in general seem about four years behind those of the same age on the Breckland. A brief visit here in mid-April 1938 showed that the distributions of species common to both areas were similar (including, incidentally, chaffinch and coal tit) provided that the trees were compared by height and not by age.

9. Factors influencing distribution

The following discussion is not intended to be exhaustive, and many species of which little is known or which were discussed in the earlier paper are omitted. Knowledge of the earlier paper and of the general discussion of factors on a psychological plane in Lack (1937) is here assumed.

(a) *Species which colonize*

The absence of the *meadow pipit* from bare brecks, and its abundance on the heaths, seem correlated with its nest site in thick ground vegetation, which is not supplied by the brecks; for it regularly feeds on bare ground and sings in the air. Nest sites also seem to limit *yellow wagtail* and *common partridge*, which are also absent from the brecks but regular on the heaths.

The *stonechat* colonizes the taller heath vegetation and the young plantations. Outside the breeding season it is regular in low heathland, and it regularly feeds on the ground and in the air, and nests in thick ground vegetation. It normally sings from a perch several feet off the ground, and this seems the chief factor supplied by the young plantations; see also Lack & Venables (1939). Song posts also seem the limiting factor for the *whinchat* and *willow warbler*; the latter, for which thick cover may also be important, is discussed in the earlier paper.

The *wren* breeds on the tallest heaths and in the young plantations, and since it is regular on low heaths outside the breeding season, it is presumably limited by a breeding factor, but more is not known. The *dunnock* shows a rather similar distribution but does not spread on to low heathland in winter, hence a breeding factor cannot be all that is involved. The dunnock and also the *whitethroat* sing several feet off the ground, nest in thick cover off the ground and in general frequent thick cover, all of which are first supplied about the fifth year after planting.

The appearance of the *blackbird* in the sixth or seventh year seems primarily correlated with its song post, for it feeds mainly on the ground. Nest sites may be a subsidiary factor, for the typical site is a few feet off the ground, but lower forks, and also the ground, are used at times. The appearance of the *robin* also seems correlated with its song post, for it nests on the ground, feeds regularly on the ground and in general seems "at home" in low cover, but it sings fairly high up. Most species only limited by song posts spread into lower vegetation in autumn and winter; the robin does not do this, but, unlike most species, it maintains a territory with song in autumn and winter. The *chiffchaff* is also limited by its song post, for it nests only a few feet off the ground, feeds regularly in lower vegetation, but sings high up; it does not colonize until the fourteenth year. The song post limitations of *tree pipit* and *wood lark* have been discussed.

So soon as breeding is over, the *coal tit* spreads into much lower plantations, showing that its summer distribution is limited by a breeding factor, and since it nests on the ground, feeds in lower plantations, but sings high up, its song post is clearly indicated. The winter distribution of the *blue tit* is similar to that of the coal tit, but it does not breed in the 12- to 15-year-old plantations where the coal tit breeds; observation shows that its song post requirements would be met here, and its nest site is clearly the limiting factor, for, unlike the coal tit, it does not nest in holes in the ground, but only in holes off the ground. The distribution of the *goldcrest* both in summer and winter is similar to that of the coal tit, hence its summer distribution is clearly limited by a breeding factor; both song post and nest site are typically high off the ground. Since it occurs in younger plantations so soon as breeding is over, nest site and/or song post, both of which are typically high off the ground, would also seem to limit the *chaffinch*. The appearance of the *ring dove* in the fourteenth year seems probably associated with its nest site; it feeds outside the plantations. The occurrence of the *pheasant* in the plantations, but not usually on the heaths, is perhaps associated with its habit of roosting in trees, for it both nests and feeds on the ground; general cover may also be important.

Hence most of the arrivals which can be analysed seem correlated with nest site or song post. The song post assumes a far greater importance here than it would in a general discussion of the limits to bird distribution; but this is to be expected, since the changes in distribution are primarily correlated with the height, not the nature, of the vegetation.

(*b*) *Species which depart*

The departures are much harder to analyse than the arrivals. Those of *wheatear* and *stock dove* are clearly associated with the disappearance of the rabbit burrows in which they nest. Nest sites are clearly not involved in the

departure of *skylark*, *meadow pipit*, *whinchat* and *stonechat*, for an adequate number of sites remains in the older plantations. Food may be important for the skylark, which eats many seeds, but the other three species have a most varied insect diet. Whitethroat and dunnock decrease markedly in the older plantations so soon as the lower branches of the pines are cut; their song posts are still present, the insect life of the pines is still present, and their nest sites are still present, though only much higher off the ground. No direct environmental factor seems to prevent whitethroat and dunnock living in the "upper storey" of the older plantations, which seems to provide conditions extremely similar to those of younger plantations. But it is the habit of both species to frequent secondary growth close to the ground, and this habit seems the important factor. However, the evidence for this general habitat selection is less clear in such cases than in others discussed in the earlier papers.

10. Summary

1. Detailed figures from walking counts are given, comparing the successive breeding and mid-winter bird populations of Breckland heaths and pine plantations from 4 to 15 years old. Both in summer and winter, the changes in the populations resulting from the increasing height of the trees are extremely striking.

2. Comparison with Schiermann's data for North German pine plantations reveals many similarities in distribution, but chaffinch and coal tit colonize the British plantations much earlier than they do the German ones.

3. The factors limiting distribution are discussed. For colonizing species, song posts and to a less extent nest sites are the most important factors.

References

Lack, D. (1933). "Habitat selection in birds, with special reference to the effects of afforestation on the Breckland avifauna." J. Anim. Ecol. 2: 239–62.

Lack, D. (1937). "The psychological factor in bird distribution." Brit. Birds, 31: 130–6.

Lack, D. & Venables, L. S. V. (1937). "The heathland birds of South Haven Peninsula, Studland Heath, Dorset." J. Anim. Ecol. 6: 62–85.

Lack, D. & Venables, L. S. V. (1939). "The habitat distribution of British woodland birds." J. Anim. Ecol. 8: 39–70.

Schiermann, G. (1934). "Studien über Siedelungsdichte im Brutgebiet. 2. Der brandenburgische Kiefernwald." J. Orn. (Leipzig), 82: 455–86.

Watt, A. S. (1936). "Studies in the ecology of Breckland. I. Climate, soil and vegetation." J. Ecol. 24: 117–38.

Appendix 1. Species omitted from Table 1 of breeding bird populations

A few species were omitted from the calculated percentages of breeding bird populations, as their occurrences were too uncertain, or (game birds and birds of prey) were greatly influenced locally by human activities. The cuckoo

(*Cuculus canorus*) is regular on the heaths in small numbers, and was occasionally seen in older plantations; several species regularly parasitized by the cuckoo breed in the plantations, but it is not known if the cuckoo actually parasitizes them there. The nightjar (*Caprimulgus europaeus*), being crepuscular, was seldom observed; it was found in a 6- and an 8-year-old plantation and is regular on some of the heaths. The mistle thrush (*Turdus viscivorus*) was common in mid-June in plantations of most ages, especially in the rides. It is not known whether it breeds regularly, since nesting is over before the season when the counts were taken. An extremely young fledgling found in a 12-year-old plantation had almost certainly come from a nest in this plantation. The short-eared owl (*Asio flammeus*) and Montagu's harrier (*Circus pygargus*) have bred in some years in plantations up to 8 years old. (The marsh tit (*Parus palustris*) recorded from an 8-year-old plantation in 1931 was an error for coal tit (*P. ater*).) The pheasant (*Phasianus colchicus*) is regular in plantations of 4 years old up to 15 years old. The red-legged partridge (*Alectoris rufa*) is regular on the bare brecks, the heaths and plantations up to about 5 years old; after that it occurs in plantations only in the rides. Similar remarks apply to the common partridge (*Perdix perdix*) save that it is absent from bare brecks.

APPENDIX 2. SPECIES OMITTED FROM TABLE 2 OF WINTER BIRD POPULATIONS

For similar reasons, various species were omitted from the percentage calculations for the mid-winter bird populations. The pheasant and the two partridges are distributed much as in the breeding season except that the pheasant is also regular on the heaths. Merlin (*Falco columbarius*), hen harrier (*Circus cyaneus*), sparrowhawk (*Accipiter nisus*) and other species of birds of prey at times hunt over the heaths and plantations. Carrion crow (*Corvus corone*), hooded crow (*C. cornix*), rook (*C. frugilegus*) and starling (*Sturnus vulgaris*) at times feed on the heaths and plantations up to 5 years old, the rook and starling being in flocks. Four goldfinches (*Carduelis carduelis*) were seen in a 5-year-old plantation; they also occurred on the very edges of other plantations. The list of casual winter visitors could be greatly extended, but the object of the present paper is to describe the distributions of the characteristic species.

THE BIRD POPULATION ON AN OXFORDSHIRE FARM[1]

By W. M. M. CHAPMAN

1. Place and times of censuses

The observations upon which this paper is based were made by members of the Oxford Ornithological Society on Temple Farm, Sandford-on-Thames, between 1926 and 1935. A census of the bird population on a typical piece of Oxfordshire farm land was originally suggested by Mr E. M. Nicholson; from 1930 onwards it was generally supervised by Mr W. B. Alexander (now Director of the Edward Grey Institute of Field Ornithology). This report has enjoyed the same supervision. In 1932 Mr Alexander published an account of the results obtained on the eastern half of this farm up to 1931 ("The bird population on an Oxfordshire farm", *J. Anim. Ecol.* (1932), 1: 58–64). The paper dealt primarily with the winter counts, those for the summer on the same area being given for comparison. In the four succeeding winters counts were made much more frequently and regularly, and it became evident that the conclusions based on the comparatively infrequent counts in the earlier winters were partly unreliable. This paper is therefore based on the results obtained in the later work (1931–5) and partly supersedes the earlier report with the same title.

Temple Farm consists (or consisted, some of it has since been built over) of some 300 acres of low level fields, lying on the left bank of the River Thames 3 miles below Oxford; it is roughly bisected by the Oxford-Henley road. The winter counts of 1926–7 to 1930–1 and 1934–5 were taken on 125 acres east of the road, consisting of pasture (except for small patches of stubble and clover in the first year or two), divided by hedges of varying height and density (2·7 miles per 100 acres) all containing oak (*Quercus*) and, predominantly, elm (*Ulmus*) trees. The eastern half includes a dry 4 acre copse, and about 8 acres of whins (*Ulex*). The winter counts of 1931–2 to 1933–4 were taken on an equal area (125 acres) west of the road. Of this about two thirds was pasture of the same type (only the fields are smaller, 3·1 miles of hedge per 100 acres), the remainder a large arable field with cottages along one side (1·25 miles of hedge per 100 acres). The western half includes two small copses totalling rather less than 1 acre. The summer counts of 1931–4 were taken on the eastern half as described; on a further 11 acres of pasture; on the western half as described, and on the water-meadows (including a wet copse) lying between the western half and the Thames. The summer area may be analysed as follows:

225 acres of pasture (8 acres of whins, 5 acres of dry copses, 6 miles of hedge).

[1] Publication of the British Trust for Ornithology.

40 acres of arable ($\frac{1}{2}$ mile of hedge).

32 acres of water-meadows (3 acres of wet copse, 1 mile of hedge, $\frac{1}{3}$ mile of river bank).

Total 297 acres: a good sample of mixed farm land with about $2\frac{1}{2}$ miles of hedge per 100 acres.

2. Validity of the sample censuses

This is an account of what was observed on one area, for what it is worth; if comparable observations can be made on other areas, they will, together, be worth much more. In the hope that such observations may be made, and may be comparable, I have given below some account of our procedure. The validity of a sample census depends upon three factors: (1) the size of the sample; (2) the methods by which figures are obtained; and (3) how these figures are handled.

(1) The size of a sample is measured in two ways. The *extension* of this census was small, in winter only 125 acres: its *intensity* was high; the last column in Table 2 is based on 86 counts spread over 10 winters. It was therefore in some sense equivalent to a single count of more than 20 square miles. We do not know what is the minimum sample area which yields any valid figures in a reasonable number of counts; it must, at any rate, include in the right proportions all the types of habitat in the area to be sampled. Nor do we know what is the largest area which it would be economical to survey; this depends on the range of the "chance" wanderings of the birds "resident" in the area. In practice, as large an area should be taken as can be adequately covered at one time. If this were found to be 60 acres of the kind of ground which I have described, and if it were possible to take 16 counts, I should be inclined, *ceteris paribus*, to take 8 counts of each of two adjacent and apparently homogeneous pieces of ground (taking precautions against counting the birds in, e.g. their common hedge, 16 times); if only 10 counts could be made, I should devote them all to one 60 acre piece. Our experience does not allow us to formulate more precise or more general rules for planning a census: it may be worth while to have indicated such rough conclusions as have been reached.

(2) *Methods*. In winter the ground was covered between 2 and 4 p.m. by a party of 6–12 observers. Their procedure was exactly that of a shooting party intent upon walking up partridges and beating the hedges for pheasants. Open fields were covered "in line", hedges taken with one observer on each side, copses "driven" (as by armed beaters who wanted their share of the shooting; birds were counted by observers both inside and outside the copse). The same route was always adopted and conferences held periodically to ensure that a blackbird, e.g. flying from one hedge to another (whether spontaneously or under provocation), had not been counted twice. The general impression was that the error was not more than 10%, and that birds counted

twice roughly balanced birds missed, though, for example, a blackbird is more likely to be counted twice, a tree-creeper to be missed. In a large number of counts an error of $\mp 10\%$ would disappear. The numbers of birds observed were entered field by field, and a record kept of the amount of hedge attributed to each field; this makes it possible in a later year to take a comparable census of *part* of the area. It was found that there was a limit to the usefulness of enduring wind and weather, for the birds didn't. It is not thought the errors caused by wrong identification were large.

The method employed in summer counts was to enter upon a map all birds apparently resident on the farm, with notes on their behaviour. This method was pursued with varying thoroughness. In 1931 the ground was only covered once. (The extra 11 acres on the east and the 40 acres arable on the west were not covered at all; averages from the other three years are inserted in the tables.) In 1932–3 it was covered twice. In 1934 an attempt was made to see whether a much more thorough survey would not yield very different figures. The area was divided into 9 small pieces and each surveyed on one or more afternoons in the 2nd, 4th, 6th and 8th weeks of University term (April–June), by the same two observers. A certain amount of checking was also done by supernumeraries. Great attention was given to the finding of nests. All observations were entered (in four coloured inks) on a map of the whole area (25 in. to 1 mile for fields, 50 in. to 1 mile for copses) from which the number of each species present was computed. So far as the commoner species are concerned, the percentage error, in an enquiry necessarily inexact, is almost certainly negligible. The figures thus obtained are reassuringly like those obtained in the three previous summers, though those for 1931 may not be very accurate. In particular the figure for song thrush is almost certainly too low. The economical method of 1932–3 (two counts, no insistence on finding nests) seems confirmed as adequate for our purpose. This does not apply to the copses, to which particular attention was given. There is something to be said for making a recount of any given area within a fortnight, but if both the early thrushes and the later warblers are to be observed this would involve four counts.

It may be worth while to give examples of the signs employed in mapping the farm in summer:

Bird apparently resident	• robin
with sex if possible	• blackbird ♂
if a bird of the year	• robin *Y*
singing cock	• wren ♂ *S*
with nesting material, food, excrement	• wren *B*, *F*, excrement
nest	× (robin)
with any contents	× (robin) 3 *E*, 1 *Y*,

this denotes a nest identified by build, eggs, or nestlings; a nest with a bird

in attendance is marked " ×chaffinch ♀ (or ♂)"; where the sex of this bird is indeterminate ♀ was assumed. This assumption was merely for marking purposes, to avoid the ambiguous mark " ×robin" (was there a bird there or does this belong to the pair seen 60 yd. × farther on?). This ambiguous sign should never occur.

Both summer (with one improper exception noted below) and winter tables take account of all birds "resident" on the area, including, for example, the hovering kestrel, but not of birds seen merely flying over (as distinct from about) the farm.

(3) The summer figures raise no problems of statistical method; we are dealing, more than less at any rate, with actual numbers of birds living on our area during the nesting season. But any winter population figure must be an average; upon how many counts should such averages be based? From a study of the figures at our disposal three conclusions seem to emerge: (*a*) In view of the fluctuations from month to month a series of six monthly averages gives a much better account of the bird population in any given winter than a single winter population average. (*b*) In view of what may be called "chance" fluctuations from count to count, an average figure for any month must be based on not less than 3 counts taken in the course of that month. The figures for the western half in 1933–4 show, I think, that a monthly average so based is reasonably valid. In this winter 4 counts a month were taken, averages based on any 3 counts do not in general greatly differ from those based on 4; averages based on any 2 counts differ very widely. The detailed figures on which this paper is based may be seen at the Edward Grey Institute. For the winters 1931–2–3 we have only 7 and 12 counts respectively; the populations of these winters can therefore only be described by single average winter population figures. (*c*) In view of both "chance" fluctuations, and fluctuations from month to month, any single winter population average should be based on, say, 2 counts a month, or at least on 9 counts taken at regular intervals. For the five winters 1926–7 to 1930–1 we have only 1, 4, 1, 7, 12 counts, taken at irregular intervals. On these records it does not seem justifiable to base more than one single winter population average for the "composite winter" 1926–31. This figure is a mean of monthly means based on the following numbers of counts: 5 Oct., 6 Nov., Dec. with 3 Jan., 8 Feb., 3 Mar.; the under-emphasis of Dec. and Jan., in 1933–4 the most populous period, may partly account for the low figure thus arrived at. (All the counts in these five winters were made on the eastern half.) From what has been said it follows that our averages must in all cases be means not medians.

The danger of accepting averages more narrowly based is well illustrated by certain figures (see Alexander, 1932) for the winters 1927–8, 1929–30, 1930–1. These figures lead almost irresistibly to two conclusions: (1) that the population is relatively constant in one winter and another; and (2) that the

fall in numbers during the winter (which we know must take place somewhere, whether or not there is a long period as well as an annual cycle in bird population) was observable to a very marked extent upon this area. More adequate observations now suggest: (1) that there are large and irregular fluctuations from one winter to another (Table 1); and (2) that no considerable decrease is observable on our area during the winter (Table 2). My own hypothesis is that this is a relatively sheltered spot, that the birds which die are, for the most part, those for which there is no room in such areas, and that the places of those which do die in such areas are rapidly filled.

My general conclusion of this section is that the figures given in the tables are reasonably valid: the sample big enough, the methods fairly accurate, the averages fairly well founded. I confess that I have applied no statistical controls, made no correlations, calculated no deviations; nor am I sure that this would be profitable. I do not think that more can be said than that the graphs of the tables are, upon the whole, less, not more erratic, than the impression received of the fluctuations in the bird population by the naturalist in the field. "To every enquiry its appropriate degree of exactitude" (Aristotle).

3. Discussion of the tables

The matter of this report lies not in the text but in the tables. Two general notes are required: (1) Numbers of birds observed (but not the number of times upon which a species was observed) are in all cases scaled to 100 acres; they are given (except in Table 3, part 3) to the nearest integer[1]; "1" denotes not $<0{\cdot}5$; "0", $<0{\cdot}5$; "–", total absence. The basis of each figure (i.e. the area covered and the number of counts) will be found in the tables or notes on them. (2) The way in which species are grouped is not that of any orthodoxy, though it nearly resembles that of the B.O.U.; it is the grouping into which the species seemed naturally to fall as we discussed their fluctuations in the field, and as I handled the figures recording these fluctuations.

Tables 1 *and* 2, *Winter*

Table 1 describes the only two winter populations of which we can give a full account, those of the western half in 1933–4, and of the eastern half in 1934–5. No account is taken, except in the totals, of species whose average was not 1 or more for one area and winter. I have no comments to make upon Table 1 that are not suggested by its perusal. The formation and dissolution of winter flocks (especially of skylarks and the finches) is well illustrated, and the steadiness of the "resident thrushes", dunnock and wren, and, in a lesser degree, tit groups, is clearly marked. The main difference between the two populations is the greater number of skylarks and finches on the western half, of which one-third was ploughed up; the dry copse on the eastern half accounts,

[1] Hence the *apparent* incorrectness of some of the figures in the totals and the summaries.

Table 1. *Winter populations* (*West*: 85 *acres pasture*, 40 *acres arable*; *East*: 125 *acres pasture*)

West, 1933–4	Times recorded out of 24	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Av.
Rook	**17**	4	2	19	14	2	1	7
Jackdaw	**4**	—	—	—	4	—	1	1
Starling	**24**	123	97	124	129	75	74	104
Chaffinch	**24**	22	32	18	20	11	29	22
House sparrow	**24**	78	50	27	19	21	20	35
Linnet	**12**	7	5	6	—	—	1	3
Greenfinch	**12**	0	1	0	1	2	1	1
Yellowhammer	**21**	23	17	10	14	0	30	16
Corn bunting	**11**	—	—	13	13	25	30	13
Skylark	**24**	23	32	50	54	63	17	40
Meadow pipit	**11**	2	3	2	5	2	3	3
Pied wagtail	**13**	1	2	1	0	2	0	1
Blue tit	**24**	4	8	6	11	10	12	8
Long-tailed tit	**14**	4	2	2	2	2	2	2
Great tit	**14**	1	1	0	1	0	2	1
Fieldfare	**16**	—	5	32	134	16	8	32
Redwing	**18**	—	7	29	17	25	11	15
Mistle thrush	**14**	—	2	3	2	1	0	1
Blackbird	**24**	25	25	25	23	23	25	24
Song thrush	**24**	13	12	13	13	10	8	11
Robin	**24**	10	10	8	5	9	7	8
Dunnock	**24**	2	4	3	4	3	5	3
Wren	**24**	4	3	3	2	4	4	3
Green woodpecker	**16**	1	0	2	0	1	1	1
Wood pigeon	**20**	2	1	0	2	3	4	2
Lapwing	**10**	4	7	0	1	1	4	3
Partridge	**20**	9	13	7	10	4	4	8
Summary								
Crows		4	2	19	18	2	2	8
Starling		123	97	124	129	75	74	104
Finches		108	88	51	40	34	50	61
Buntings		23	17	23	27	25	59	29
Lark, pipit, wagtail		26	37	53	60	67	20	44
Tits		9	10	8	15	12	16	12
Winter thrushes[1]		—	14	64	152	42	20	49
Resident thrushes[2]		47	47	46	41	42	41	44
Dunnock, wren		6	7	6	6	7	9	7
Non-passerine		16	21	9	14	9	13	14
Total (all species)		367	345	406	504	319	303	374

East, 1934–5	Times recorded out of 18	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Av.
Rook	**14**	2	0	1	23	2	12	7
Carrion crow	**13**	4	2	3	0	1	4	2
Jackdaw	**6**	1	—	—	6	—	2	2
Magpie	**15**	2	2	1	5	1	2	2
Jay	**13**	1	1	2	1	2	2	2
Starling	**18**	107	82	68	107	227	126	120
Chaffinch	**18**	9	8	21	21	10	9	13
House sparrow	**18**	16	19	40	15	12	14	19
Greenfinch	**17**	13	13	19	15	3	1	11
Goldfinch	**12**	6	1	4	1	2	2	2
Bullfinch	**12**	0	0	2	3	1	1	1
Yellowhammer	**17**	4	6	27	29	10	15	15
Skylark	**9**	3	0	1	11	2	—	3
Blue tit	**18**	5	6	8	6	6	5	6
Long-tailed tit	**15**	14	11	8	7	2	4	8
Great tit	**14**	1	1	1	3	1	1	2
Marsh tit	**11**	5	1	1	2	1	1	2
Fieldfare	**13**	5	18	80	27	59	8	33
Redwing	**10**	—	1	4	0	8	7	3
Blackbird	**18**	30	26	54	35	37	39	37
Song thrush	**18**	4	14	15	11	9	4	10
Robin	**18**	12	12	15	19	11	14	14
Dunnock	**18**	1	2	4	2	2	4	3
Wren	**18**	3	4	4	3	1	2	3
Green woodpecker	**16**	3	2	2	1	1	2	2
Wood pigeon	**14**	7	11	0	10	12	18	10
Lapwing	**4**	5	—	—	8	—	60	12
Partridge	**18**	9	9	23	17	9	8	13
Summary								
Crows		10	5	7	35	7	22	14
Starling		107	82	68	107	227	126	120
Finches		44	41	85	55	27	27	46
Buntings		4	6	27	29	10	15	15
Lark, pipit, wagtail		3	0	1	11	2	—	3
Tits		26	19	18	18	10	11	17
Winter thrushes[1]		5	19	84	27	68	15	36
Resident thrushes[2]		47	52	85	65	57	58	61
Dunnock, wren		5	6	8	5	4	6	6
Non-passerine		24	22	23	36	22	88	36
Total (all species)		280	255	410	394	437	373	360

[1] Including mistle thrush. [2] And robin.

Table 2. *Winter populations*

Part 1. Average numbers of commoner species

Index no.	Name	East, 125 acres pasture: 1926–31 (25 counts)	1934–5 (18 counts)	Times recorded out of 43	Mean for 1926–31 and 1934–5	West, 85 acres pasture: 1931–2 (7 counts)	1932–3 (12 counts)	1933–4 (24 counts)	Times recorded out of 43	Mean for 1931–2–3–4	West, 40 acres arable: 1931–2 (7 counts)	1932–3 (12 counts)	1933–4 (24 counts)	Times recorded out of 43	Mean for 1931–2–3–4	East and west pasture: Times recorded out of 86	Mean of E. and W. (pasture)
1	Rook (*Corvus frugilegus*)	10	7	**26**	9	10	12	8	**29**	10	23	2	7	**12**	11	**55**	9
2	Carrion crow (*Corvus corone*)	1	2	**25**	2	1	2	1	**12**	1	3	5	0	**11**	2	**37**	1
3	Jackdaw (*Corvus monedula*)	0	2	**9**	1	1	0	1	**7**	1	2	0	0	**4**	1	**16**	1
4	Magpie (*Pica pica*)	0	2	**25**	1	—	0	1	**8**	0	—	—	—	**0**	—	**33**	1
5	Jay (*Garrulus glandarius*)	1	2	**24**	1	—	0	—	**1**	0	—	—	—	**0**	—	**25**	1
6	Starling (*Sturnus vulgaris*)	62	120	**38**	91	123	130	113	**42**	122	84	35	100	**38**	73	**80**	106
7	Chaffinch (*Fringilla coelebs*)	9	13	**43**	11	18	23	23	**43**	21	48	290	22	**42**	120	**86**	16
8	House sparrow (*Passer domesticus*)	1	19	**26**	10	63	23	31	**42**	39	140	45	48	**39**	78	**68**	25
9	Linnet (*Carduelis cannabina*)	6	1	**19**	3	5	3	4	**16**	4	150	138	3	**22**	97	**35**	4
10	Greenfinch (*Chloris chloris*)	5	11	**33**	8	5	2	2	**22**	3	1	8	0	**8**	3	**55**	5
11	Goldfinch (*Carduelis carduelis*)	2	2	**20**	2	6	2	1	**8**	3	—	1	1	**4**	1	**28**	3
12	Bullfinch (*Pyrrhula pyrrhula*)	1	1	**20**	1	1	0	1	**10**	0	—	—	0	**1**	0	**30**	1
13	Tree sparrow (*Passer montanus*)	0	0	**5**	0	0	—	—	**1**	0	1	3	0	**7**	1	**6**	0
14	Yellowhammer (*Emberiza citrinella*)	14	15	**35**	15	29	10	23	**38**	21	1	1	6	**14**	3	**73**	18
15	Corn bunting (*Emberiza calandra*)	0	0	**2**	0	—	—	20	**11**	7	—	—	3	**2**	1	**13**	3
16	Skylark (*Alauda arvensis*)	3	3	**17**	3	23	1	8	**26**	10	108	44	110	**41**	87	**43**	7
17	Meadow pipit (*Anthus pratensis*)	3	0	**18**	2	9	1	3	**17**	5	5	—	3	**8**	3	**35**	3
18	Pied wagtail (*Motacilla alba*)	0	0	**5**	0	—	0	—	**3**	0	2	—	3	**13**	2	**8**	0
19	Blue tit (*Parus caeruleus*)	4	6	**38**	5	13	10	11	**43**	11	7	5	5	**31**	5	**81**	8
20	Long-tailed tit (*Aegithalos caudatus*)	2	8	**25**	5	2	2	3	**20**	3	—	2	1	**5**	1	**45**	4
21	Great tit (*Parus major*)	2	2	**29**	2	5	4	1	**26**	3	2	3	1	**16**	2	**55**	2
22	Marsh tit (*Parus palustris*)	1	2	**18**	1	1	0	0	**7**	0	—	—	—	**0**	—	**25**	1
23	Tree-creeper (*Certhia familiaris*)	1	1	**15**	1	1	0	1	**10**	0	—	—	0	**2**	0	**25**	1
24	Fieldfare (*Turdus pilaris*)	7	33	**23**	20	34	21	48	**26**	34	18	1	5	**10**	8	**49**	27
25	Redwing (*Turdus musicus*)	2	3	**18**	3	13	4	20	**27**	12	4	5	7	**11**	5	**45**	8
26	Mistle thrush (*Turdus viscivorus*)	1	0	**12**	1	5	2	2	**25**	3	1	2	2	**12**	1	**37**	2
27	Blackbird (*Turdus merula*)	28	37	**43**	33	47	47	31	**43**	42	23	41	14	**42**	26	**86**	37
28	Song thrush (*Turdus ericetorum*)	6	10	**42**	8	33	17	14	**43**	22	14	26	7	**39**	16	**85**	15
29	Robin (*Erithacus rubecula*)	6	14	**43**	10	31	18	11	**43**	20	8	5	4	**38**	6	**86**	15
30	Dunnock (*Prunella modularis*)	2	3	**37**	2	3	5	4	**39**	4	2	2	2	**16**	2	**76**	3
31	Wren (*Troglodytes troglodytes*)	3	3	**41**	3	4	5	5	**41**	5	3	1	2	**15**	2	**82**	4
32	Green woodpecker (*Picus viridis*)	1	2	**30**	1	1	1	1	**25**	1	1	—	—	**1**	0	**55**	1
33	Lapwing (*Vanellus vanellus*)	7	12	**13**	10	6	3	2	**12**	4	18	21	4	**9**	14	**25**	7
34	Wood pigeon (*Columba palumbus*)	10	10	**32**	10	6	3	2	**34**	4	9	1	1	**13**	4	**66**	7
35	Stock dove (*Columba oenas*)	2	0	**7**	1	0	0	0	**3**	0	0	2	0	**2**	1	**10**	1
36	Partridge (*Perdix perdix*)	6	13	**41**	9	6	4	8	**30**	6	8	16	9	**18**	11	**71**	8
37	Species in Part 2	3	3	...	3	1	1	1	...	1	1	0	1	...	1	...	2

Part 2. Number of times on which uncommon species were recorded

38	Brambling (*Fringilla montifringilla*)	—	—	—	...	1	—	—	**1**	...	—	1	—	**1**	...	**1**	...
39	Reed bunting (*Emberiza schoeniclus*)	2	1	**3**	...	4	2	—	**6**	...	1	—	—	**1**	...	**9**	...
40	Cirl bunting (*Emberiza cirlus*)	—	—	—	...	—	—	1	**1**	...	—	—	—	—	...	**1**	...
41	Grey wagtail (*Motacilla cinerea*)	—	—	—	...	—	1	—	**1**	...	—	—	—	—	...	**1**	...
42	Cole tit (*Parus ater*)	1	—	**1**	...	—	—	2	**2**	...	—	—	—	—	...	**3**	...
43	Willow tit (*Parus atricapillus*)	?	?	**?**	...	—	—	—	—	...	—	—	—	—	...	**?**	...
44	Goldcrest (*Regulus regulus*)	4	2	**6**	...	—	2	—	**2**	...	—	—	—	—	...	**8**	...
45	Nuthatch (*Sitta europaea*)	—	—	—	...	—	—	1	**1**	...	—	—	—	—	...	**1**	...
46	Stonechat (*Saxicola torquata*)	4	1	**5**	...	—	—	—	—	...	—	—	—	—	...	**5**	...
47	Gr. sp. woodpecker (*Dryobates major*)	3	—	**3**	...	—	—	1	**1**	...	—	—	—	—	...	**4**	...
48	Lr. sp. woodpecker (*Dryobates minor*)	1	—	**1**	...	—	2	1	**3**	...	—	—	1	**1**	...	**4**	...
49	Barn owl (*Tyto alba*)	3	1	**4**	...	—	—	—	—	...	—	—	—	—	...	**4**	...
50	Tawny owl (*Strix aluco*)	1	7	**8**	...	—	—	2	**2**	...	—	—	—	—	...	**10**	...
51	Little owl (*Athene noctua*)	8	9	**17**	...	1	3	5	**9**	...	—	—	—	—	...	**26**	...
52	Peregrine (*Falco peregrinus*)	—	—	—	...	—	—	3	**3**	...	—	—	—	—	..	**3**	...
53	Kestrel (*Falco tinnunculus*)	8	8	**16**	...	1	1	4	**6**	...	—	1	2	**3**	...	**22**	...
54	Sparrow hawk (*Accipiter nisus*)	2	2	**4**	...	1	—	1	**2**	...	—	—	—	—	...	**6**	...
55	Mallard (*Anas platyrhynchus*)	5	2	**7**	...	—	—	—	—	...	—	—	1	**1**	...	**7**	...
56	Teal (*Querquedula crecca*)	—	2	**2**	...	—	—	—	—	...	—	—	—	—	...	**2**	...
57	Heron (*Ardea cinerea*)	1	1	**2**	...	—	1	3	**4**	...	—	—	1	**1**	...	**6**	...
58	Common snipe (*Capella gallinago*)	10	—	**10**	...	1	1	—	**2**	...	—	—	—	—	...	**12**	...
59	Jack snipe (*Lymnocryptes minimus*)	—	—	—	...	1	—	—	**1**	...	—	—	—	—	...	**1**	...
60	Domestic pigeons (*Pigeones domesticatae*)	—	—	—	...	—	—	—	—	...	—	—	4	**4**	...	**0**	...
61	Moorhen (*Gallinula chloropus*)	5	1	**6**	...	—	1	—	**1**	...	—	—	—	—	...	**7**	...
62	Pheasant (*Phasianus colchicus*)	14	10	**24**	...	1	2	1	**4**	...	—	—	—	—	...	**28**	...

Part 3. Summary

Crows (1–5)	12	14	...	13	12	14	10	...	12	26	7	7	...	13	...	13
Starling (6)	62	120	...	91	123	130	113	...	122	84	35	100	...	73	...	106
Finches (7–13, 38)	24	47	...	36	97	53	61	...	70	340	485	73	...	299	...	53
Buntings (14, 15, 39, 40)	14	15	...	15	29	10	43	...	27	1	1	8	...	3	...	21
Lark, pipit, wagtails (16–18, 41)	6	3	...	5	32	3	11	...	15	114	44	116	...	91	...	10
Tits, etc. (19–23, 42–45)	10	18	...	14	21	17	15	...	18	8	10	6	...	8	...	16
Winter thrushes (24–26)	11	37	...	24	52	28	69	...	50	22	7	14	...	15	...	37
Resident thrushes (27–29, 46)	39	61	...	51	111	82	56	...	83	44	72	24	...	47	...	67
Dunnock, wren (30, 31)	5	6	...	5	7	10	8	...	8	5	3	4	...	4	...	7
Non-passerine (32–36, 47–62)	28	39	...	34	21	11	15	...	16	36	39	15	...	30	...	25
Total all species (1–62)	212	360	...	286	504	357	401	...	421	681	702	369	...	584	...	354

in winter as in summer, for its higher figures for magpie, jay, bullfinch, owls, and wood-pigeon.

Table 2 compares single average winter population figures for five winters, two on the eastern half and three on the western half. The pasture and arable areas on the western half are treated separately. The first part of the table deals only, except in the last line, with species whose average on any one area (east, west pasture, west arable) in any one winter was 1 or more. The second part gives the *number of times* that other species were recorded. The third is a summary of the first (and so in its last line of the second [1]). The total pasture populations, if the not very satisfactory figure [2] in the first column be ignored, vary between 3·6 and 5·0 birds per acre. The total arable populations, which consist principally of large flocks of finches and skylarks, are rather higher, and are subject to rather greater fluctuation, 3·7–7·0 birds per acre. It will be seen that the species which in this table show relatively little fluctuation from year to year, are those which, in Table 1, show relatively little fluctuation from month to month. They are the hedge association, "resident thrushes", dunnock and wren, and the tits. Further, they are about equally numerous on pasture and on arable. For although their figures, calculated (as in Table 2) per 100 acres, are lower on arable; if calculated per mile of hedge they would be very similar. (The hedge per 100 acres attributed to the arable area is only about half that of the pasture.)

Table 3, *Summer*

Table 3 compares the populations of the whole farm in the four summers 1931–4. The first part deals (to the nearest integer) with all species whose mean figure for the four summers is 1 or more. The second gives (to the nearest tenth) the mean figures for the four summers of all other species recorded, and the number of summers in which they occurred. Though there are more species (31/58) these make up only 6% of the average total population. The third part is a summary of the first two, and takes account of the numbers in each year of the species dealt with in the second part.

I have worked out separate figures for the three types of ground into which the summer area is divided (pasture, arable, water-meadows; see introductory

[1] Or rather, of the unprinted fractional figures for the species dealt with in Part 2, corresponding with the figures in Part 1.

[2] It is almost certainly too low, see p. 289. The facts there given will not, indeed, account for the whole difference between the populations of the eastern half in 1926–31 and 1934–5. It is possible that the establishment of roosts of fieldfares and finches (mainly house sparrow) in the interval, may to some small extent account for the higher total of the later winter, for counts were taken in the afternoon and a certain number of fieldfares and finches may have been counted which were resident on the farm rather by night than by day. But this will not account for the general increase (see blackbird, robin, tits and other species). Nor are we able to assign any differences in weather or crops as the causes of similar increases and decreases on the western half in the winters 1932–3–4.

Table 3. *Summer populations*, 1931–4 (297 *acres*)

Part 1

Index no.	Name	1931	1932	1933	1934	Mean
1	Carrion crow (*Corvus corone*)	3	1	3	1	2
5	Starling (*Sturnus vulgaris*)	5	2	3	10	5
6	Chaffinch (*Fringilla coelebs*)	25	24	28	23	25
7	Linnet (*Carduelis cannabina*)	6	8	13	14	10
8	House sparrow (*Passer domesticus*)	4	5	11	10	7
9	Yellowhammer (*Emberiza citrinella*)	9	6	9	5	7
10	Greenfinch (*Chloris chloris*)	3	2	2	3	3
16	Skylark (*Alauda arvensis*)	5	1	3	4	3
17	Tree pipit (*Anthus trivialis*)	2	2	2	1	2
20	Blue tit (*Parus caeruleus*)	3	2	4	7	4
21	Long-tailed tit (*Aegithalos caudatus*)	2	1	2	4	2
22	Great tit (*Parus major*)	2	2	1	2	2
27	Whitethroat (*Sylvia communis*)	11	7	12	11	10
28	Lesser whitethroat (*Sylvia corruca*)	1	1	1	1	1
29	Garden warbler (*Sylvia borin*)	2	2	0	1	1
30	Willow wren (*Phylloscopus trochilus*)	4	3	1	4	3
31	Chiffchaff (*Phylloscopus collybita*)	4	2	2	2	2
35	Blackbird (*Turdus merula*)	37	36	41	42	39
36	Song thrush (*Turdus ericetorum*)	12	22	21	22	19
37	Robin (*Erithacus rubescens*)	12	10	12	8	11
38	Whinchat (*Saxicola rubetra*)	1	2	1	1	1
42	Dunnock (*Prunella modularis*)	7	6	8	7	7
43	Wren (*Troglodytes troglodytes*)	7	10	6	6	7
51	Lapwing (*Vanellus vanellus*)	1	3	5	6	4
53	Moorhen (*Gallinula chloropus*)	3	4	3	2	3
54	Wood pigeon (*Columba palumbus*)	9	3	5	9	6
57	Partridge (*Perdix perdix*)	1	0	2	2	1

Part 2

Index no.	Name	No. of summers in which present	Mean 1931–4
2	Jackdaw (*Corvus monedula*)	1	0·3
3	Magpie (*Pica pica*)	3	0·9
4	Jay (*Garrulus glandarius*)	3	0·4
11	Goldfinch (*Carduelis carduelis*)	2	0·3
12	Bullfinch (*Pyrrhula pyrrhula*)	2	0·3
13	Tree sparrow (*Passer montanus*)	2	0·6
14	Corn bunting (*Emberiza calandra*)	3	0·4
15	Reed bunting (*Emberiza schoeniclus*)	2	0·3
18	Pied wagtail (*Motacilla alba*)	1	0·1
19	Yellow wagtail (*Motacilla flava*)	1	0·1
23	Marsh tit (*Parus palustris*)	4	0·7
24	Willow tit (*Parus atricapillus*)	1	0·1
25	Cole tit (*Parus ater*)	2	0·3
26	Tree creeper (*Certhia familiaris*)	3	0·4
32	Spotted flycatcher (*Muscicapa striata*)	3	0·7
33	Blackcap (*Sylvia atricapilla*)	3	0·7
34	Sedge warbler (*Acrocephalus schoenobaenus*)	3	0·5
39	Mistle thrush (*Turdus viscivorus*)	4	0·8
40	Redstart (*Phoenicurus phoenicurus*)	1	0·3
41	Nightingale (*Luscinia megarhyncha*)	3	0·2
44	Green woodpecker (*Picus viridis*)	3	0·6
45	Cuckoo (*Cuculus canorus*)	3	0·4
46	Kingfisher (*Alcedo atthis*)	2	0·3
47	Tawny owl (*Strix aluco*)	2	0·3
48	Little owl (*Athene noctua*)	4	0·6
49	Kestrel (*Falco tinnunculus*)	2	0·3
50	Mallard (*Anas platyrhyncha*)	1	0·1
52	Snipe (*Capella gallinago*)	3	0·3
55	Stock dove (*Columba oenas*)	1	0·1
56	Turtle dove (*Streptopelia turtur*)	2	0·3
58	Pheasant (*Phasianus colchicus*)	2	0·3
	Total		12·0

Part 3

		1931	1932	1933	1934	Mean
1–4	Crows	5	1	4	3	4
5	Starling	5	2	3	10	5
6–15	Finches, buntings	50	45	65	58	54
16–19	Lark, pipit, wagtails	6	3	5	5	5
20–26	Tits, creeper	10	7	8	14	10
27–34	Warblers	25	15	19	20	20
35–41	Thrushes	68	70	77	73	71
42–43	Dunnock, wren	14	16	14	13	14
44–58	Non-passerine	17	13	21	22	18
	Total (all species)	198	172	215	217	200

Part 3 is a summary of Parts 1 and 2 (i.e. it takes into account the annual figure not printed for species in Part 2). The figures in the "mean" columns have only to be divided by 2 to yield the percentage, for the species or group in question, of the total population.

section), but it is not worth while to print these details. It does indeed appear from them that the water-meadows were a little richer than the rest of the area, that the warblers (except whitethroat) were found in the copses, and the kingfisher's nest in the river bank. But no differences are found comparable to the difference between pasture and arable populations in winter. The summer population seems to be fairly evenly spread out and to depend rather on length and density of hedges (the copses are little more than grown-up hedges) than upon acreage. Much the most striking thing about summer population is the extremely close correlation between any two summers, its constancy.

One comment must be made: it may be taken from the absence of, for example, rook, that all passengers were excluded, for though rooks did not nest, they did, of course, feed on the farm. Such exclusion would clearly be improper; it is possible that a considerable proportion of the summer population may consist of non-breeding birds, stationary or wandering. In general any bird seen on the farm was marked down; those not seen again were counted, in 1934, for example, when 4 counts were made, as $\frac{1}{4}$. But rooks, and to a lesser extent, jackdaws, swifts, swallows, house martins and lapwings, which could be known not to be breeding, were in some years arbitrarily excluded. The omission of rook is not of any importance, for the number of counts made in summer could not be supposed to yield a valid average for a species visiting the farm irregularly in fairly large numbers. The rook census of 1931 gives the summer population for the Upper Thames area as 14 per 100 acres.

Tables 4 *and* 5, *Summer and Winter compared*

It may be worth while, if only to show how little correlation there is between them, to compare the populations on the same area in consecutive summers and winters. Table 4 is a comparison (not abstractable from the other tables printed) (*a*) of the eastern half (pasture) summer 1934 with the following winter; (*b*) of the western half, pasture, summers 1932, 1933, 1934, with the respectively previous winters; (*c*) of the western half, arable, mean summer population 1932–4 with mean winter population 1931–4. This last area seems too small, and the fluctuations in its population too large, to give more than a mean figure. It will be seen that on pasture the summer is a little more than half the total winter population. On arable the summer appears to be only a quarter of the winter population; but the arable area had only half as much hedge per 100 acre as the pasture. If I am right in thinking that arable winter population depends chiefly on acreage, and that summer population, on arable as on pasture, depends chiefly on the amount of hedge, then we may conclude that on arable with $2\frac{1}{2}$ miles of hedge per 100 acres the

Note: Except in the summaries of groups and the totals, no note is taken in Table 4 of species with figures less than 1 for the subdivisions of the area.

Table 4. *Summer and winter comparisons*

	East 125 acres pasture		West 85 acres pasture								West 40 acres arable	
	W. 1934–5	S. 1934	W. 1931–2	S. 1932	W. 1932–3	S. 1933	W. 1933–4	S. 1934	W. mean	S. mean	W. mean 1931–4	S. mean 1932–4
Carrion crow	2	**2**	1	—	2	**3**	1	—	1	**1**	2	—
Magpie	2	**5**	—	—	0	—	1	—	0	—	—	—
Jay	2	**2**	—	—	0	—	—	—	0	—	—	—
Starling	120	**7**	123	**5**	130	—	113	**21**	122	**9**	73	**4**
Chaffinch	13	**16**	18	**30**	23	**25**	23	**31**	21	**29**	120	**16**
House sparrow	19	**1**	63	—	23	**1**	31	**21**	39	**7**	78	**17**
Linnet	1	**11**	5	**16**	3	**19**	4	**23**	4	**19**	97	**9**
Greenfinch	11	**3**	5	**3**	2	**1**	2	**5**	3	**3**	3	**3**
Bullfinch	1	—	1	—	0	—	1	—	0	—	0	**2**
Goldfinch	2	—	6	—	2	—	1	—	3	—	1	—
Tree sparrow	0	**1**	0	—	—	—	—	—	0	—	1	—
Yellowhammer	15	**7**	29	**11**	10	**16**	23	**6**	21	**11**	3	**3**
Corn bunting	0	—	—	—	—	**1**	20	—	7	**0**	1	**2**
Reed bunting	0	**2**	0	—	0	—	—	—	0	—	0	—
Skylark	3	**3**	23	**4**	1	**8**	8	**10**	10	**7**	87	**2**
Meadow pipit	0	—	9	—	1	—	3	—	5	—	3	—
Tree pipit	—	**0**	—	**1**	—	—	—	—	—	**0**	—	—
Pied wagtail	0	—	—	—	0	—	—	—	0	—	2	—
Blue tit	6	**5**	13	**1**	10	**1**	11	**11**	11	**5**	5	**1**
Long-tailed tit	8	**4**	2	**1**	2	—	3	**3**	3	**1**	1	**3**
Great tit	2	**0**	5	**1**	4	**3**	1	**2**	3	**2**	2	**2**
Marsh tit	2	**0**	1	—	0	—	0	—	0	—	—	—
Willow tit	0	**1**	—	—	—	—	—	—	—	—	—	—
Tree creeper	1	—	1	—	0	—	1	**0**	0	**0**	0	**0**
Fieldfare	33	—	34	—	21	—	48	—	34	—	8	—
Redwing	3	—	13	—	4	—	20	—	12	—	5	—
Mistle thrush	0	—	5	**1**	2	—	2	**1**	3	**1**	1	**2**
Song thrush	10	**11**	33	**26**	17	**35**	14	**30**	22	**30**	16	**18**
Blackbird	37	**31**	47	**50**	47	**55**	31	**57**	42	**54**	26	**35**
Robin	14	**6**	33	**18**	18	**14**	11	**6**	20	**12**	6	**6**
Whinchat	—	**2**	—	—	—	—	—	—	—	—	—	—
Nightingale	—	**1**	—	—	—	—	—	—	—	—	—	—
Dunnock	3	**7**	3	**8**	5	**15**	4	**4**	4	**9**	2	**4**
Wren	3	**1**	4	**11**	5	**3**	5	**8**	5	**7**	2	**3**
Blackcap	—	**1**	—	—	—	—	—	—	—	—	—	—
Garden warbler	—	**2**	—	—	—	—	—	—	—	—	—	—
Willow wren	—	**4**	—	—	—	—	—	**3**	—	**1**	—	**2**
Chiffchaff	—	**2**	—	—	—	**1**	—	—	—	**0**	—	—
Whitethroat	—	**13**	—	**10**	—	**18**	—	**13**	—	**13**	—	**7**
Lesser whitethroat	—	**2**	—	**3**	—	—	—	—	—	**1**	—	—
Green woodpecker	2	**2**	1	—	1	—	1	—	1	—	0	—
Cuckoo	—	**0**	—	—	—	**1**	—	—	—	**0**	—	**1**
Little owl	0	**2**	0	**3**	0	**1**	0	—	0	**1**	—	—
Kestrel	0	**0**	0	**1**	0	—	0	—	0	**0**	0	—
Lapwing	12	**8**	6	**8**	3	**10**	2	**10**	4	**9**	14	—
Wood pigeon	10	**16**	6	**6**	3	**4**	2	**4**	4	**5**	4	**3**
Stock dove	0	—	0	—	0	—	0	**1**	0	**0**	1	—
Moorhen	0	—	—	**3**	0	**3**	—	—	0	**2**	0	—
Partridge	13	**3**	6	**1**	4	—	8	**1**	6	**1**	8	—
Pheasant	0	**2**	0	—	0	—	0	—	0	—	—	—
					Summary							
Crows	7	**9**	2	—	2	**3**	2	—	2	**1**	2	—
Starling	120	**7**	123	**5**	130	—	113	**21**	122	**9**	73	**4**
Finches	47	**32**	97	**49**	53	**46**	61	**80**	70	**58**	299	**47**
Buntings	15	**9**	29	**11**	10	**17**	43	**6**	27	**11**	3	**5**
Lark, pipits, wagtail	3	**3**	32	**5**	3	**8**	11	**10**	15	**8**	91	**2**
Tits, creeper	18	**10**	21	**3**	17	**4**	15	**16**	18	**8**	8	**6**
Thrushes	98	**51**	163	**95**	110	**104**	125	**94**	133	**97**	62	**61**
Dunnock, wren	6	**8**	7	**19**	10	**18**	8	**12**	8	**16**	4	**7**
Warblers	—	**24**	—	**13**	—	**19**	—	**16**	—	**16**	—	**9**
Non-passerine	39	**33**	21	**22**	11	**19**	15	**16**	16	**19**	30	**4**
Total (all species)	353	**186**	494	**222**	345	**238**	393	**271**	411	**243**	573	**145**

proportion of winter to summer population would have been not very much higher than the proportion found on pasture, say 5 : 2.

Finally, if we consider the whole area covered in both summer and winter (that is, the summer area as described, less the water-meadows and 11 acres pasture on the east side), and if we quote as the "winter population" for this area a mean of the average winter population on the eastern half and the average winter population on the western half, we find that the numbers (of those species whose average summer or winter figure is 1 or more) compare as follows (Table 5). The source of the summer figure for rook is given above. The reader is reminded that figures are given per 100 acres and to the nearest integer; "0" denotes $<0{\cdot}5$.)

Table 5. *Comparison of average populations (per hundred acres) in winter and summer*

Species	Winter	Summer	Species	Winter	Summer
Fieldfare	23	—	Greenfinch	5	2
Meadow pipit	3	—	Long-tailed tit	4	2
Redwing	6	—	Dunnock (hedge sparrow)	3	7
Starling	98	5	Wren	3	5
Blackbird	35	36	Carrion crow	2	2
Chaffinch	32	21	Corn bunting	2	0
House sparrow	31	7	Great tit	2	1
Linnet	19	11	Goldfinch	2	0
Skylark	19	4	Mistle thrush	2	1
Yellowhammer	15	8	Green woodpecker	1	1
Song thrush	14	17	Jay	1	0
Robin	13	9	Magpie	1	1
Rook	10	14	Chiffchaff	—	1
Lapwing	8	5	Lesser whitethroat	—	1
Partridge	8	1	Whinchat	—	1
Blue tit	7	2	Whitethroat	—	11
Wood pigeon	7	6	Willow wren	—	2

4. Summary

Winter censuses of the bird population on areas of 125 acres in the Thames Valley near Oxford between 1926 and 1935 (86 counts) show the composition of the bird population and the limits within which it fluctuated. The species most regular from month to month, from winter to winter, and from pasture to arable land, were those dependent on the hedges; the least regular were the finches, found mainly in large flocks on arable. The total winter population varied, on pasture (2·7 miles of hedge per 100 acres) from 3·6 (omitting one record, for reasons given above) to 5·0 birds per acre; on arable from 3·7 to 7·0 birds per acre. (Throughout this paper "arable" means, of course, arable surrounded by pasture; on a purely arable area a very different population might be found.) Two tables showing the population month by month in single winters show rather the "chance" fluctuations of the "arable" species, and the formation and dissolution of winter flocks, than any decrease during the course of the winter.

Summer censuses of the bird population on about 300 acres of the same farm in 1931, 1932, 1933 and 1934 show the composition of the summer population and its constancy. It appears that in summer the regularity which in winter is found only in the hedge association is extended to almost all species. There was little variation from summer to summer, or from pasture to arable land. The average total population was 2 birds per acre.

A comparative table shows no correlation between the populations of consecutive summers and winters. On the average, on the same ground, the winter was roughly double the summer population.

THE NOCTURNAL ACTIVITY OF CRANE-FLIES (TIPULINAE) AS INDICATED BY CAPTURES IN A LIGHT TRAP AT ROTHAMSTED

By A. G. ROBERTSON

(*Department of Entomology, Rothamsted Experimental Station*)

(*With Plate* 11 *and* 8 *Figures in the Text*)

CONTENTS

		PAGE
1.	Introduction	300
2.	Numbers captured	301
3.	Sex proportions	302
4.	Distribution	303
	(*a*) Monthly distribution	303
	(*b*) Distribution throughout the night	310
5.	Influence of temperature on nocturnal activity	314
6.	Influence of cloud and moonlight on activity	319
7.	Summary	321
8.	Acknowledgements	322
	References	322

1. Introduction

Figures obtained by catching insects in a light trap at Rothamsted Experimental Station, Harpenden, form the basis of this study of the nocturnal activity of crane-flies of the sub-family Tipulinae (Diptera). The group was selected because of the economic importance of the larvae of a number of its species—notably *Tipula paludosa*, *T. oleracea* and *Pales flavescens*—and also because it was captured in numbers large enough to allow of statistical analysis of the influence of various climatic factors on its activity.

The light trap, its construction, situation and method of working have been described by Williams (1935). It was kept in use continuously (with occasional accidental stoppages), for four years—March 1933 to February 1937. The captures of Tipulinae during the first two years have been analysed by Pinchin & Anderson (1936). The present study is a continuation and extension of their work. A further two years' captures have been analysed and the results for the whole four years summarized.

It is important to remember that throughout this work the term "activity" is used in the sense of phototropic activity, i.e. the number of insects caught in response to light-trapping.

2. Numbers captured

(a) Number of species

During the first two years (1933 and 1934[1]), the total number of species of Tipulinae captured in the Rothamsted light trap was 11. In the succeeding two years (1935 and 1936) this number has been increased to 17, though none of the "new" species has been captured in anything but extremely small numbers. The common species, i.e. the first seven species occurring in Table 1, are still the same as in the first two years, viz.:

1. *Tipula paludosa* Meig.
2. *T. obsoleta* Meig.
3. *Pales maculata* Meig.
4. *P. flavescens* Linn.
5. *Tipula pagana* Meig.
6. *T. marmorata* Meig.
7. *T. oleracea* Linn.

Table 1

Species	1933 No.	1933 % of total Tipulinae	1934 No.	1934 % of total Tipulinae	1935 No.	1935 % of total Tipulinae	1936 No.	1936 % of total Tipulinae	1933–6 No.	1933–6 % of total Tipulinae
T. paludosa	787	62·6	505	60·4	288	46·7	369	53·9	1949	57·4
T. obsoleta	159	12·6	138	16·5	89	14·4	102	14·9	488	14·4
P. maculata	129	10·3	87	10·4	19	3·1	24	3·5	259	7·6
P. flavescens	20	1·6	36	4·3	119	19·3	54	7·9	229	6·7
T. pagana	63	5·0	33	3·9	47	7·6	51	7·5	194	5·7
T. marmorata	43	3·4	22	2·6	17	2·8	45	6·6	127	3·7
T. oleracea	51	4·1	11	1·3	22	3·6	29	4·2	113	3·3
T. cava	—	—	—	—	7	1·1	4	0·6	11	0·3
T. luteipennis	4	0·3	—	—	—	—	—	—	4	0·1
T. fascipennis	—	—	2	0·2	2	0·3	—	—	4	0·1
T. vernalis	—	—	2	0·2	—	—	2	0·3	4	0·1
T. lunata	—	—	—	—	2	0·3	2	0·3	4	0·1
T. lateralis	—	—	—	—	3	0·5	1	0·1	4	0·1
T. variipennis	1	0·1	—	—	—	—	—	—	1	—
T. nigra	—	—	—	—	1	0·2	—	—	1	—
T. czizeki	—	—	—	—	1	0·2	—	—	1	—
T. peliostigma	—	—	—	—	—	—	1	0·1	1	—
All species	1257	—	836	—	617	—	684	—	3394	—
All species (excluding *T. paludosa*)	470	—	331	—	329	—	315	—	1445	—

Table 1, giving the yearly catches of each of the 17 species, has been arranged in order of total abundance of the separate species over the period of four years. Of the two genera represented, *Tipula* includes 15 species and the *Pales* only two. It is a curious fact that the greatest number of species in any one year—13—was recorded in 1935, the year of least abundance of individuals.

[1] For convenience the periods are referred to by the year in which the greater number of months falls, e.g. 1933 is really March 1933–February 1934, and so with the other three periods.

(*b*) *Numbers of each species*

The figure for the total catch per year is by no means constant, being very much larger in 1933 than in any of the succeeding three years (see Table 1). During the last two years, in fact, the combined total capture was only slightly greater than that of the first year alone. The differences between the yearly totals are very largely accounted for by fluctuation in the catch of *T. paludosa*, which was by far the most numerous species in any year. When the total catch was highest—1257 in 1933—the percentage of *T. paludosa* attained its greatest value of 62·6, and when the total catch was lowest—617 in 1935—the percentage of *T. paludosa* was reduced to 46·7, its smallest value. If the catches of *T. paludosa* are omitted, the numbers of all other species combined are seen to be very much more uniform. The figure is still rather higher for 1933, the year of greatest abundance, but practically constant in the following three years.

The ten rarer species never account for more than 2·6 % of the total catch in any one year, and for the whole four years account for only 1 % of the total.

3. Sex proportions

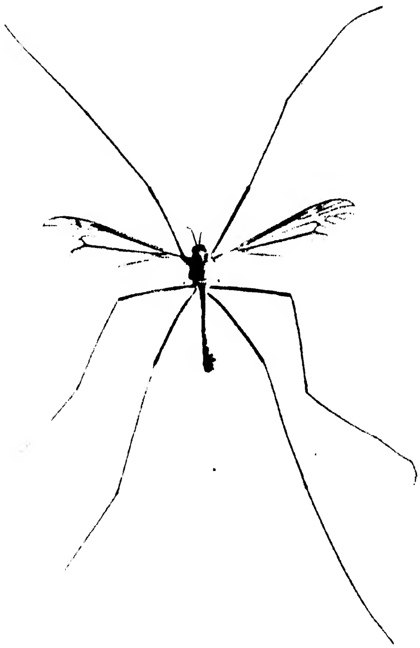
(*a*) *All Tipulinae*

Table 2, giving the proportions in which the sexes were captured, shows that in general the males of Tipulinae appear at light in greater numbers than the females. Although this holds true for the group as a whole it by no means holds for the individual species. In three of the "common" species

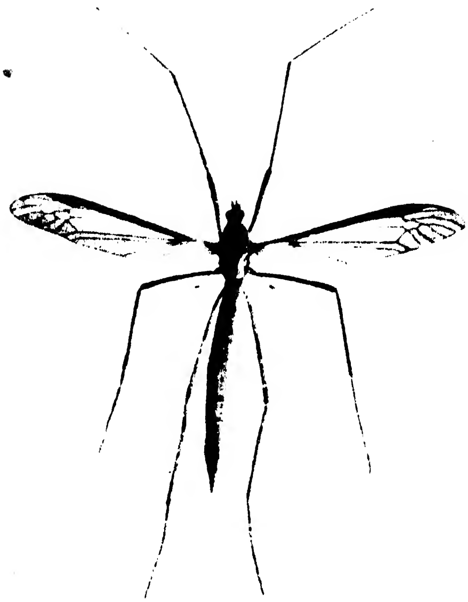
Table 2

Species	1933 Sex ratio ♂ : ♀	1933 % ♂♂	1934 Sex ratio ♂ : ♀	1934 % ♂♂	1935 Sex ratio ♂ : ♀	1935 % ♂♂	1936 Sex ratio ♂ : ♀	1936 % ♂♂	1933–6 Sex ratio ♂ : ♀	1933–6 % ♂♂
T. paludosa	578 : 209	73·4	413 : 92	81·8	209 : 79	72·6	188 : 181	50·9	1388 : 561	71·2
T. obsoleta	33 : 126	20·8	29 : 109	21·0	24 : 65	27·0	50 : 52	49·0	136 : 352	27·9
P. maculata	124 : 5	96·1	86 : 1	98·9	15 : 4	78·9	22 : 2	91·7	247 : 12	95·4
P. flavescens	18 : 2	90·0	26 : 10	72·2	107 : 12	89·9	45 : 9	83·3	196 : 33	85·6
**T. pagana*	63 : 0	100·0	33 : 0	100·0	47 : 0	100·0	51 : 0	100·0	194 : 0	100·0
T. marmorata	4 : 39	9·3	2 : 20	9·1	1 : 16	5·9	9 : 36	20·0	16 : 111	12·6
T. oleracea	9 : 42	17·6	5 : 6	45·5	9 : 13	40·9	6 : 23	20·7	29 : 84	25·7
T. luteipennis	4 : 0	—	—	—	—	—	—	—	4 : 0	—
T. fascipennis	—	—	2 : 0	—	1 : 1	—	—	—	3 : 1	—
T. vernalis	—	—	2 : 0	—	—	—	1 : 1	—	3 : 1	—
T. variipennis	1 : 0	—	—	—	—	—	—	—	1 : 0	—
T. cava	—	—	—	—	0 : 7	—	1 : 3	—	1 : 10	—
T. lateralis	—	—	—	—	0 : 3	—	0 : 1	—	0 : 4	—
T. lunata	—	—	—	—	1 : 1	—	1 : 1	—	2 : 2	—
T. nigra	—	—	—	—	1 : 0	—	—	—	1 : 0	—
T. czizeki	—	—	—	—	0 : 1	—	—	—	0 : 1	—
T. peliostigma	—	—	—	—	—	—	1 : 0	—	1 : 0	—
All species	834 : 423	66·3	598 : 238	71·5	415 : 202	67·1	375 : 309	54·8	2222 : 1172	65·4
All species (excluding *T. paludosa*)	256 : 214	54·5	185 : 146	55·9	206 : 123	62·6	187 : 128	59·4	834 : 611	57·7

* Females are wingless.



Phot. 1.



Phot. 2.

Phot. 3.

Phots. 1–3. *Tipula paludosa*. 1. Male. 2. Female. 3. Part of catch from the light-trap.

the males are more common at light than the females; in the other three the more "active" sex is the female. (In *T. pagana* only males are captured, since the females are wingless.)

The percentage of males in a year's catch varies between 71·5 (1934) and 54·8 (1936), mean 65·4. The fluctuations in this quantity are found, as in the total numbers of all species, to be largely caused by *T. paludosa*. If *T. paludosa* is omitted, the variability from year to year is very much reduced, the percentage of males then fluctuating between 62·6 and 54·5.

(*b*) *Separate species*

The species, other than *T. paludosa*, in which males are captured more abundantly than females are *Pales maculata*, *P. flavescens* and *Tipula pagana*. In the last-named species the female has only rudimentary wings and therefore cannot be captured in the trap. (As a matter of interest a single female specimen of *T. pagana* was captured in 1935. It is surmised that the insect either crawled into the trap or that it may possibly have been carried to the light by the male during the act of mating. This one specimen has not been included in any of the tables.) The three species in which females are in excess are *Tipula obsoleta*, *T. marmorata*, and *T. oleracea* with male percentages of 27·9, 12·6 and 25·7.

In the seven commonest species over the four-year period there are no values for the percentage of males between 27·9 and 71·2. In other words the sex which predominates, whether it be male or female, always accounts for more than two-thirds of the total catch. There is then in each species a marked tendency for one sex to predominate over the other.

4. DISTRIBUTION

(*a*) *Monthly distribution*

(1) *All Tipulinae.*

Tipulinae spend the winter in the larval stage underground—as the well-known leatherjackets—and imagines were never captured in the light trap between the middle of November and the beginning of May. Every year the first appearance of a Tipulinid took place some time in May, the dates for the four years being respectively 6, 20, 5 and 22 May. In November, the last month of appearance of any species, the latest date of capture was the 16th in 1936. During the four years the total catch of all species for this latter month amounted to no more than nine specimens.

Instead of actual numbers, in many of the subsequent calculations logarithms have been used. By this means it has been found possible to arrive at a more accurate estimation of the relationships which exist between insect activity and the various climatic factors. On this system, if n be the actual numerical catch for a single night, or in some cases for a single period of one

night, the value of log $(n+1)$ is taken as a measure of the catch. Unity is added to the numerical value to avoid the use of "minus-infinity" (the logarithm of 0), when the catch is zero. When the logarithms have to be reconverted into numbers the anti-logarithm is taken and unity subtracted from it. The method of using logarithms instead of numbers has been explained by Williams (1935, 1937). Its great advantage lies in the fact that any

Monthly distribution of all Tipulinae

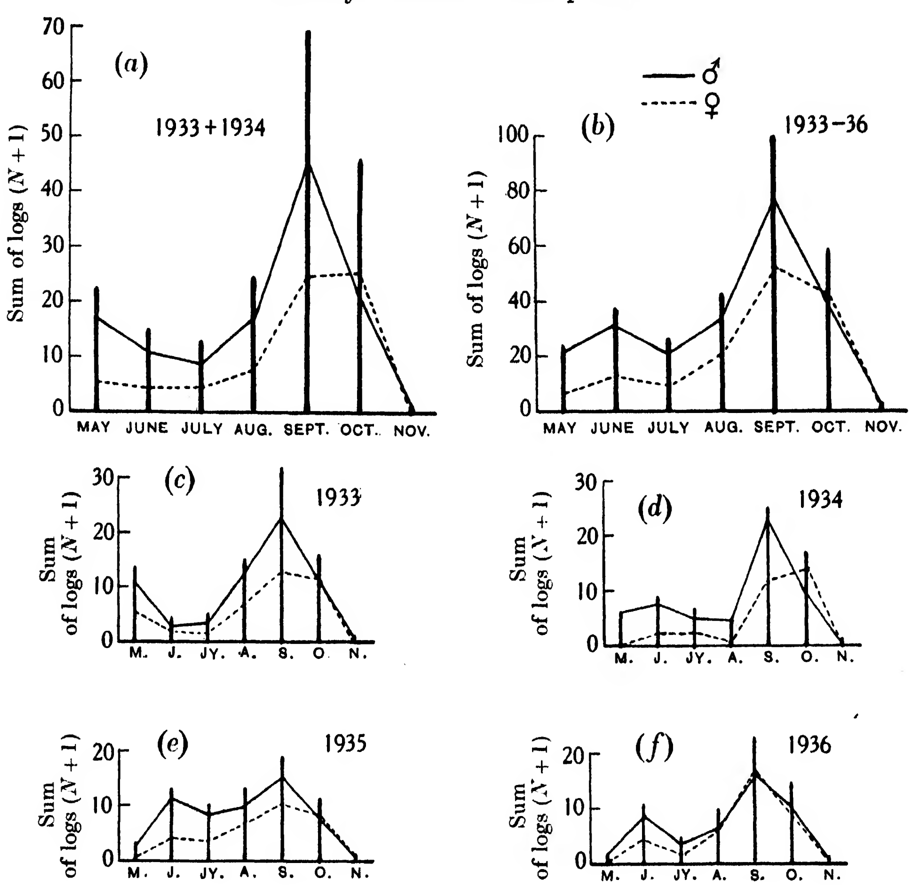


Fig. 1.

swamping effect introduced by a single very large catch is eliminated, and in every case in which they have been applied logarithms have been found to give more consistent results than numerical values.

A histogram of the monthly catches (using logarithms) by Pinchin & Anderson based on the first two years' figures showed a minor maximum in May and a major peak in September. (Reproduced in Fig. 1 (*a*).) The May peak was due to captures of *P. maculata*, and the latter to large numbers of *T. paludosa*. The addition to this diagram of the captures for a further two years has the effect of transferring the minor maximum from May to June, while the much greater September maximum is retained (Fig. 1 *b*). The change

in the month of the first maximum is due to the much greater abundance of *Pales flavescens* (chiefly active in June), in 1935 and 1936, and a great reduction in the catches of the May-flying *P. maculata.* A histogram has been drawn for each year (Fig. 1 *c–f*) and it is seen that only in 1933 was there a minor maximum in May. In all other years the diagram approximates more closely to the four-year diagram with the first peak in June. July is throughout a month of reduced frequency, the interval occurring between the maxima of activity of *P. flavescens* and *T. paludosa.*

Lines have been superimposed on the histograms to indicate the proportion of each sex in the monthly catches. As would be expected, with the general predominance of the male sex, the "male-line" approximates much more closely to the form of the histogram than does the "female-line". October is seen to be the only month in which, in general, females predominate over males. This is caused by the occurrence in October of the two species *T. marmorata* and *T. obsoleta* in which females are always captured in excess of males. There was a slight predominance of females over males observed in August and September of 1936 which was due to an increase in the proportion of females of *T. paludosa* in that year.

(2) *Separate species.*

The dates of capture of the seven common species in each of the four years are set out in Fig. 2. With the two exceptions of *T. oleracea*, which appears in all seven months from May to November, and *T. paludosa*, with a somewhat shorter range, each species has a comparatively well-defined period of activity as an imago. Particularly noticeable in this respect are the three autumn species, *T. marmorata*, *T. obsoleta* and *T. pagana.*

Tipula oleracea first appears in May or early June. It continues to be captured in small numbers for the succeeding five or six months. In each year there is evidence that the species is two-brooded, the interval between broods occurring in either July or August. In Fig. 3*a* an attempt has been made, by combining the captures for the four separate years, to determine the periods of greatest activity for the species. The days of the months of activity have been set out horizontally and the length of each vertical column represents the four-year sum of the numerical captures of *T. oleracea* for the corresponding date. By superimposing a seven-day running mean on the diagram, it can be seen that there is evidence in favour of double-broodedness in *T. oleracea.* The first brood seems to attain a period of greatest activity between the middle of May and the end of June—the second between mid-August and the end of September. In each case the appearance of a brood seems to be, on an average, comparatively evenly distributed over a period of one and a half months.

Pales maculata is usually the first species to be captured in any one year. The mean date for *P. maculata* is 14 May and for *T. oleracea* 20 May. Unlike *T. oleracea*, *P. maculata* has a comparatively short and very much more clearly defined period of activity. With the exception of a single specimen caught on 22 July 1935 (Fig. 2) the period of activity of this species was confined to May and June, the mean date of last appearance being 27 June. Fig. 3*b* shows a rapid rise to a maximum in the second half of May, followed by a gradual falling off until the end of June.

Dates of occurrence of common Tipulinae in light-trap

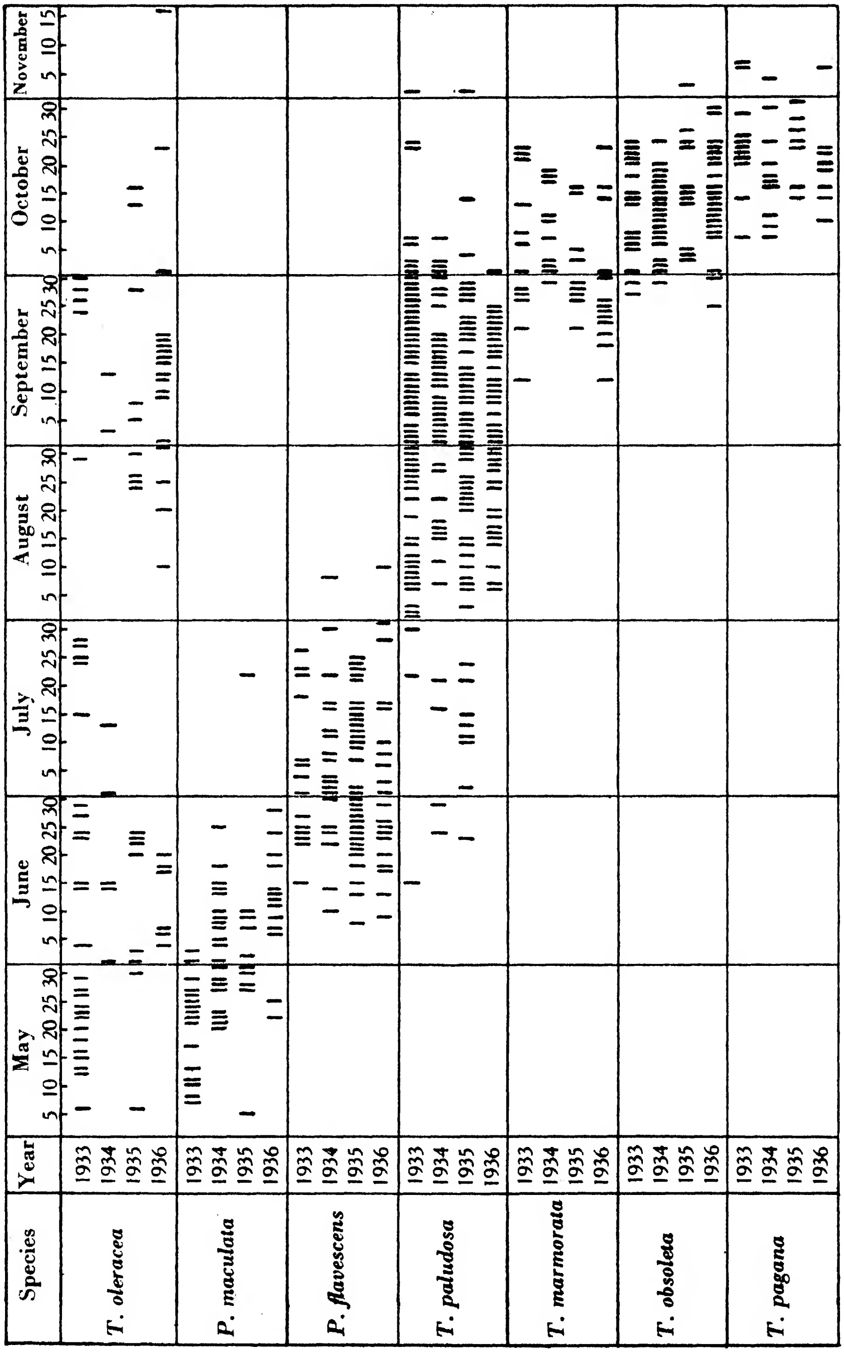


Fig. 2.

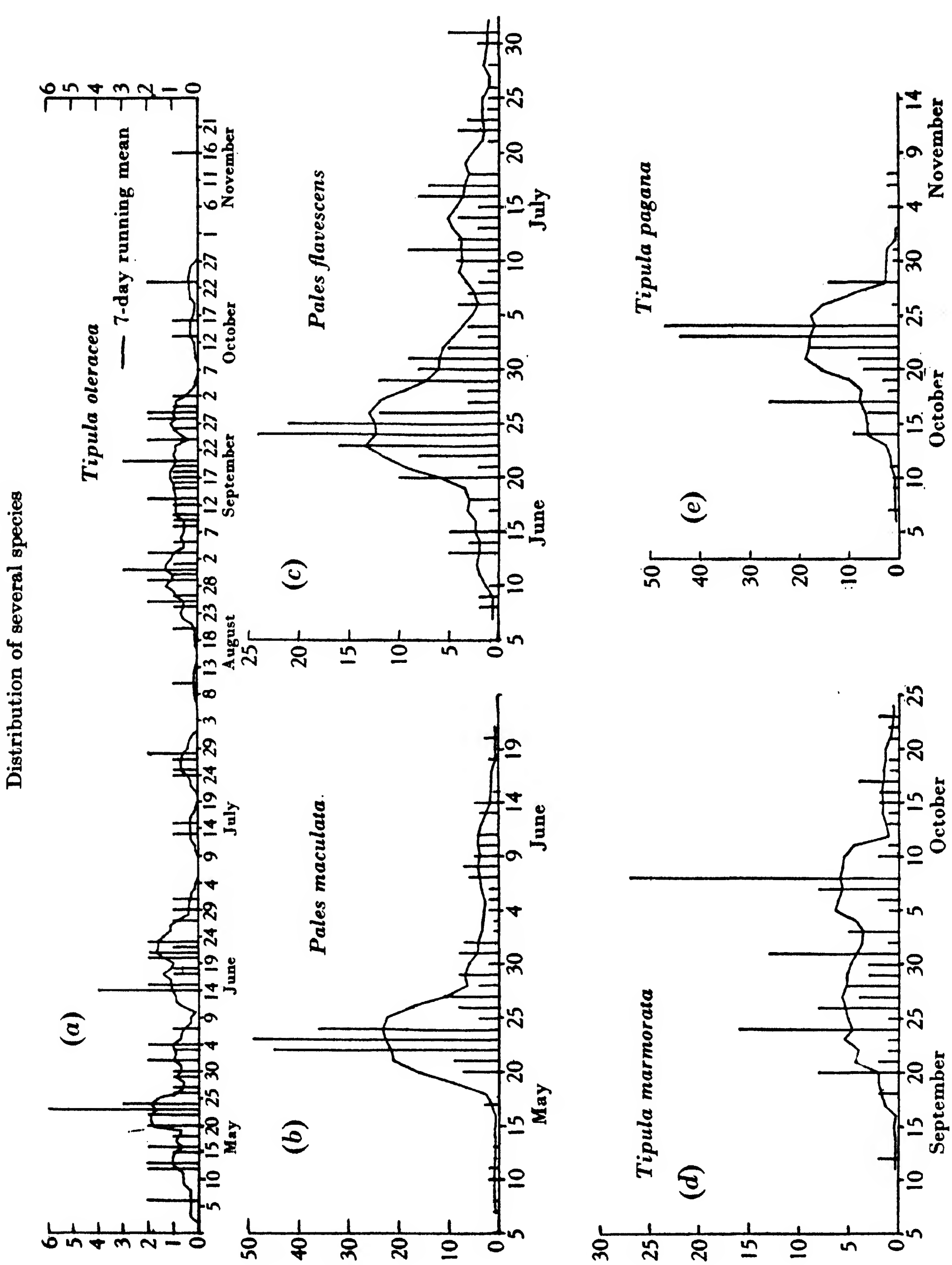

Distribution of several species
(a)
Tipula oleracea
— 7-day running mean
(b)
Pales maculata
(c)
Pales flavescens
(d)
Tipula marmorata
(e)
Tipula pagana
May
June
July
August
September
October
November

Fig. 3.

Pales flavescens is another species whose imaginal activity seems to be confined to a period of almost exactly two months. In this case the months are June and July, the mean dates of first and last appearance—11 June and 2 August—being about one month later than the corresponding dates for *P. maculata*. In distribution of activity *P. flavescens* is again very similar to the preceding species: a rapid increase in the catch in the middle of June, a maximum towards the end of the month, but a much more gradual decrease until the end of the following month—in this case July. The maximum for *P. flavescens* is not quite so sharply defined as for *P. maculata*, and the decrease is more gradual (see Fig. 3*c*).

With **Tipula paludosa** the period of activity is again comparatively long. Between the mean date of first (2 July) and last (19 October) appearances the species is active for about three and a half months. It is possible that this length is due to there being two broods of *T. paludosa* in the year. But there is little, if any, evidence in support of this view to be gained from the dates of capture of the species. No distinct break, such as is evident in the case of *T. oleracea*, can be distinguished at any particular time in the period of activity (see Fig. 2). While the distribution does not afford any positive evidence of a double brood, it does not preclude the possibility that there are two broods of *T. paludosa* in the year.

Although specimens of *T. paludosa* are captured in June and July (possibly representatives of a small first brood), the main frequency of the species is confined to August and September, when it reaches great abundance, being about four times as numerous as the next most common species. Of the four-year total of 1949, only 101 specimens were taken in other months. 16 of the latter occurred in June and July, and 85 in October and November (including a catch of 44 on 1 October 1933).

Since *T. paludosa* and *T. obsoleta* were the two most numerous species, their annual distributions have been set out in Fig. 4 in addition to their four-year distributions, to show the extent to which the periods of greatest activity of a species vary from year to year.

For *T. paludosa* the smoothed four-year diagram shows a peak not far removed from 14 September. The increase takes place gradually from the middle of August; the decrease appears to be more rapid and there is little activity after the first week in October.

Tipula marmorata, the first of the three single-brooded autumn species, had an average period of activity of 32 days between mean dates 18 September and 20 October. The maximum seems to occur somewhere between 24 September and 10 October, during which period there was no very pronounced peak during the four years under consideration (Fig. 3*d*).

Tipula obsoleta with an average length of brood of exactly one month—28 September to 28 October—attained greatest abundance some 16 or 17 days later than *T. marmorata*. The peak in *T. obsoleta* is slightly more marked than in the latter species, and appears to be somewhere between 15 and 22 October (Fig. 4).

Tipula pagana, the last of the common species, besides being notable for the rudimentary wings of the female, appears also to be remarkable for the shortness of its period of activity. Between mean dates 9 October and 4 November the average period of capture was 26 days. It never appeared before 7 October or later than 7 November. A well-defined maximum, clearly indicated by the seven-day running mean preceded by a rapid rise and succeeded by a rapid fall, occurred within one or two days of 21 October (Fig. 2).

(3) *Separate sexes.*

In an attempt to discover whether there is any difference in the seasonal occurrence of the separate sexes the two species *T. paludosa* and *T. obsoleta* were selected. In addition to being the two most numerous, these species happen to be the only two which provided sufficient numbers of both sexes for this purpose.

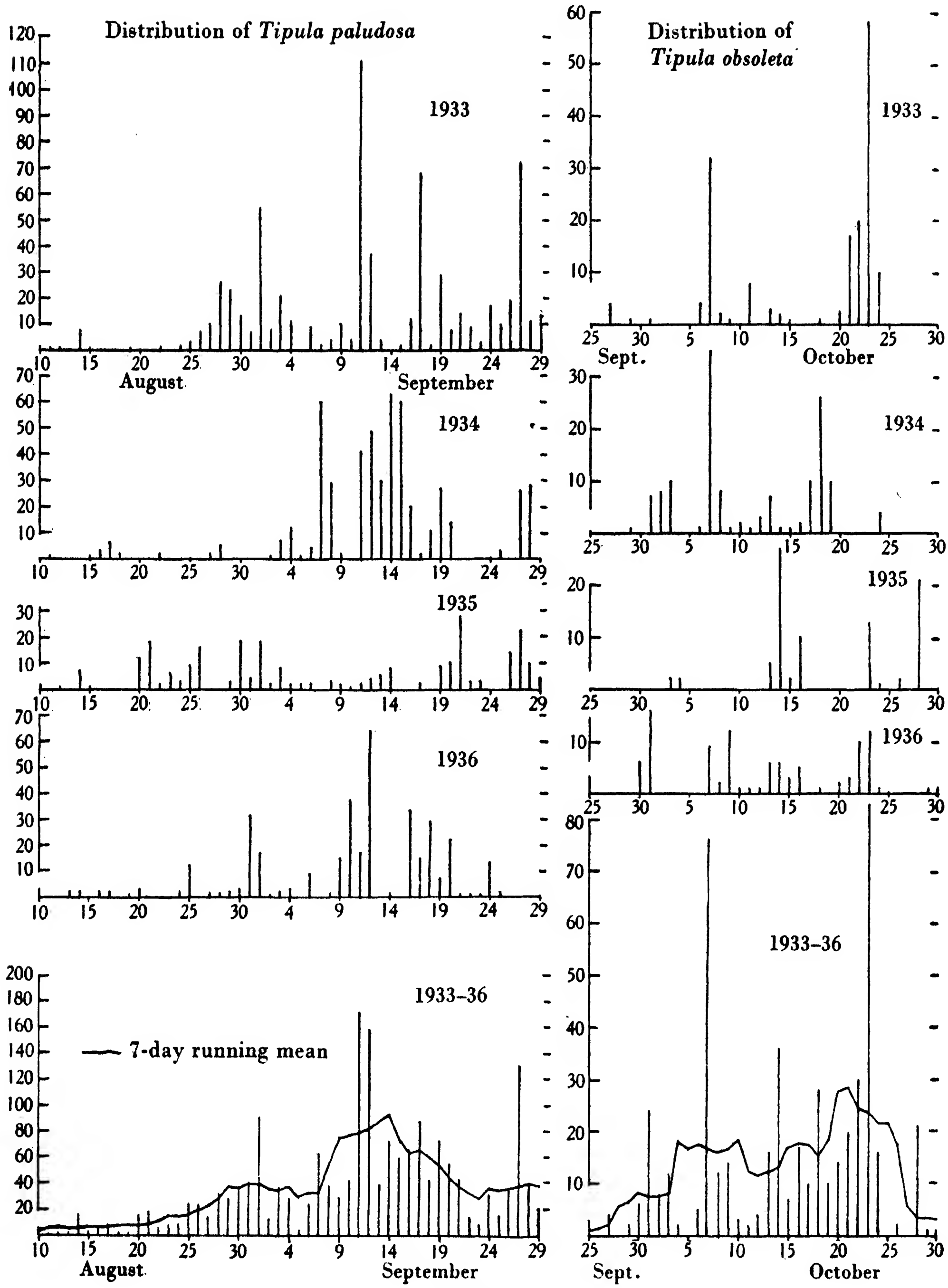

Distribution of *Tipula paludosa*
1933
1934
1935
1936
1933–36
7-day running mean
August
September
Distribution of *Tipula obsoleta*
1933
1934
1935
1936
1933–36
Sept.
October

Fig. 4.

Fig. 5 shows a seven-day running mean of the captures of each sex in each of these two species.

The graphs for *T. paludosa* indicate a close similarity in the periods of activity of the two sexes. It also shows that when the species is most active, i.e. in the middle of September, the proportion of males is at its highest. On either side of the maximum, i.e. at either end of the month, the proportions of the sexes are much more nearly equal. Whereas the peak for the males is very definitely marked, the activity of the females seems to remain at a comparatively constant level between dates around 29 August and of 19 September.

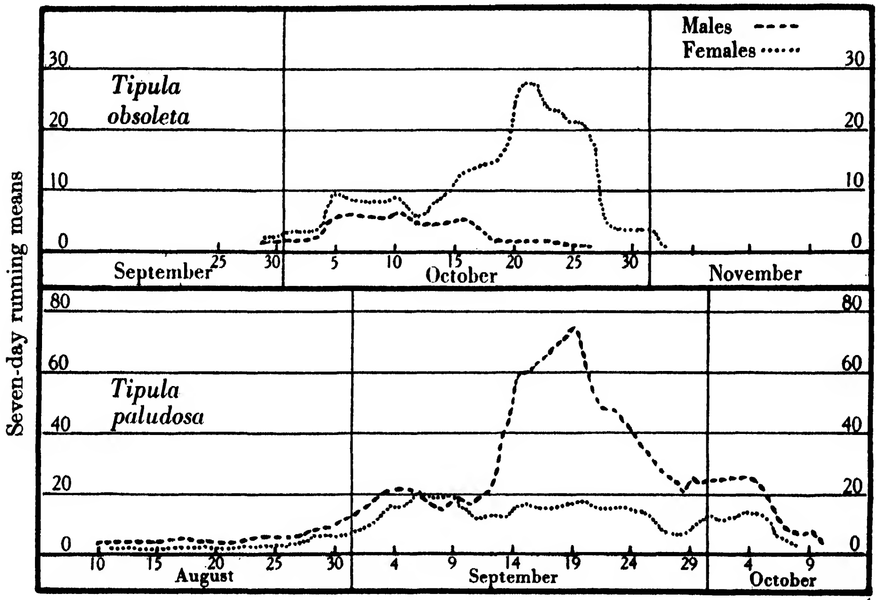


Fig. 5.

With *T. obsoleta* the story is very different. Here it is found that one sex definitely precedes the other in time of maximum activity. In this species females are captured in much greater abundance than males, and the activity of the former does not reach a maximum until some 11 days after that of the latter. The dates of maximum are about 21 October for females and 10 October for males. Both sexes make their first appearance in the trap at about the same time, but the activity of the male has decreased almost to zero before the female reaches its peak.

(*b*) *Distribution throughout the night*

(1) *All Tipulinae.*

By means of a series of eight killing-bottles and a clockwork bottle-changing mechanism, the light trap divided up the catch of insects for each night into eight successive equal portions. The night is considered to start half an hour after sunset and end half an hour before sunrise. It is therefore

possible, by studying the catches in successive periods, to investigate the distribution of activity of any species throughout the night.

For the Tipulinae as a whole the distribution of activity during the night is illustrated by Fig. 6. The maximum of activity is observed in the period immediately after sunset, the following period showing a slight reduction. During periods 3 and 4 there is a rapid fall in activity until midnight. For the second half of the night—from midnight to dawn—the activity is maintained at a fairly steady minimum level with a slight increase towards sunrise.

The separate sexes display considerable differences in behaviour. Except that the activity of the males appears to be equally distributed over the first

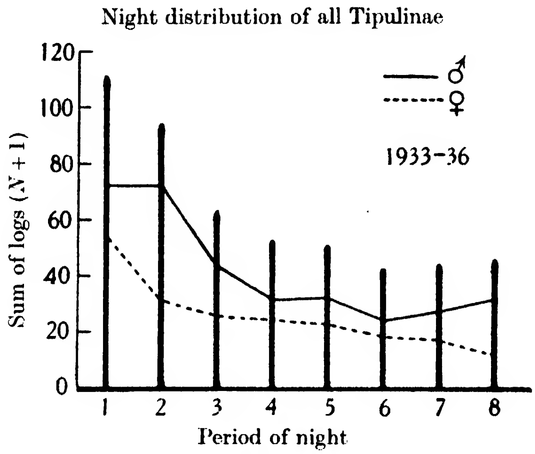


Fig. 6.

two periods their distribution follows very closely the distribution for the two sexes combined. The females, on the other hand, show a very marked peak of activity in the first period, after which an almost continuous very gradual decrease take place throughout the remaining hours of the night.

(2) *Separate species.*

Taking the individual species in turn:

Pales maculata (Fig. 7*a*) shows a very evident maximum of abundance immediately after sunset with a continuous and rapid fall until midnight. Thereafter a more or less constant low level of abundance is maintained until dawn. The very small numbers of females captured were confined almost entirely to the first half of the night.

T. oleracea (Fig. 7*b*) shows no marked period of maximum activity. Probably the total numbers captured were not large enough to establish any definite distribution. The females maintain a steady distribution throughout all but the first and last periods, at which times it is slightly less active. There is possibly a peak of activity for this sex at midnight. Males were most active just after sunset.

Pales flavescens (Fig. 6*c*), displays greatest activity in the two periods midway between sunset and midnight. There follows a sudden fall after period 3 and irregular distribution from then until dawn, with evidence of a minimum half-way between midnight and sunrise. Females in this species again account for but a small percentage (6·7) of the total, and

display no definite peak of activity. A peak, if it does exist, probably coincides with that of the males.

T. paludosa (Fig. 8) very closely resembles the total Tipulinae. A decidedly large proportion of this species is captured in the first two periods of the night. Thereafter is a sudden fall in activity until just before midnight, a more gradual fall during the next three periods and a definite increase as dawn approaches. For males the maximum is attained in the period commencing about 1½ hr. after, instead of immediately after, sunset and the rest of

Night distribution of several species over period 1933–6

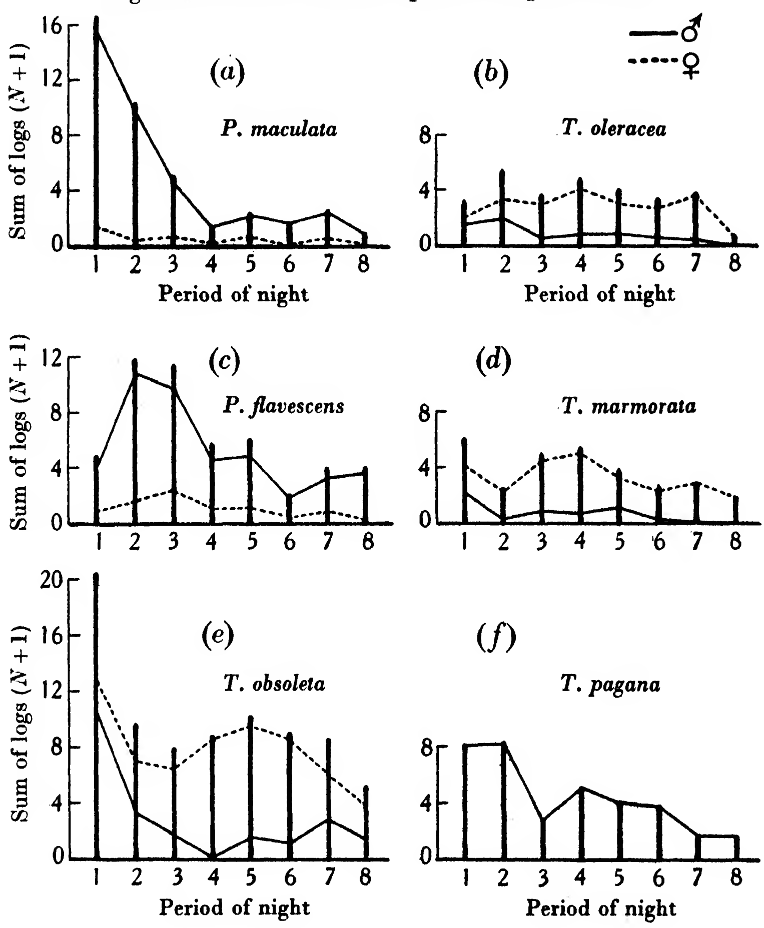


Fig. 7.

the distribution is closely similar to that of the species as a whole. The females attain a very definite maximum slightly earlier than the males, followed by a very sudden fall in period 2 and a further gradual decrease until sunrise.

T. marmorata (Fig. 7*d*) like *T. oleracea*, shows a comparatively uniform night activity. There is a definite maximum immediately after sunset, a slight fall in activity in the succeeding period, a secondary maximum at midnight and a further continuous fall until dawn. From diagrams for the four separate years it is found that the evidence for one maximum immediately after sunset and for another in the region of midnight is quite definite in every case. This applies to the females as well as to the species as a whole. The distribution of the small number of males is similar, with the secondary maximum slightly later than for the females.

T. obsoleta (Fig. 7 *e*) is very similar to *T. marmorata*. By comparison *T. obsoleta* shows an even more definite maximum just after sunset, while the secondary maximum occurs somewhat later—about an hour after midnight. The females again being greatly in the majority, have a similar distribution to the species as a whole. But the males differ notably in that the maximum activity in period 1 is followed by a minimum at or about midnight and a secondary

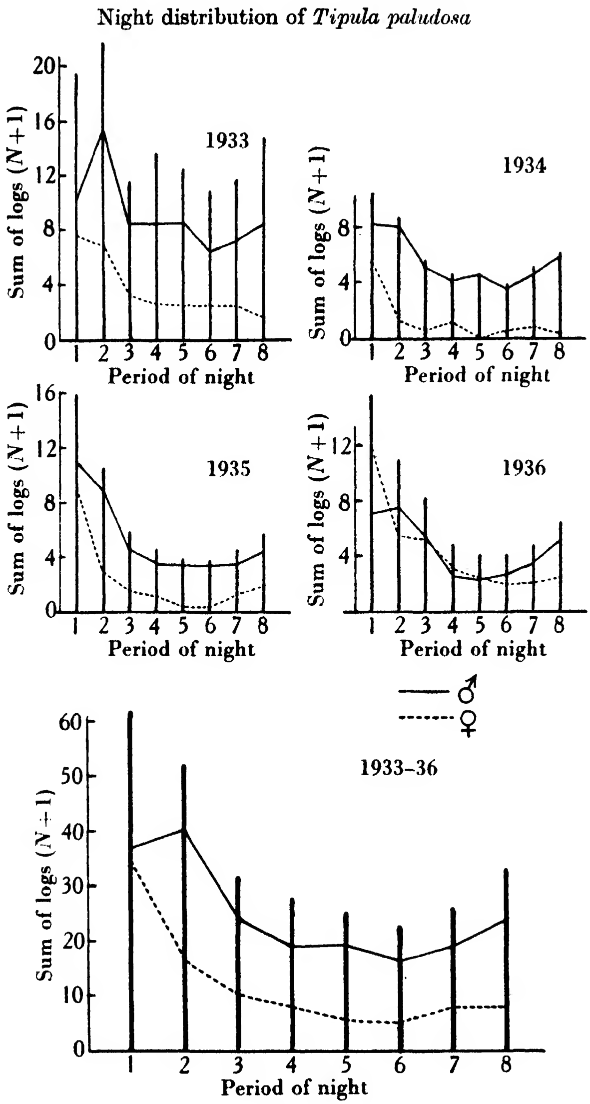


Fig. 8.

maximum in period 7. Here again yearly diagrams bring out the consistency of the two maxima, one at sunset and another which varies in "period" from 5 to 7. In general this secondary maximum occurs shortly after midnight.

T. pagana (Fig. 7 *f*), shows on the whole no very marked preference for any particular period of the night. In the usual way the first part of the night sees its greatest abundance but after period 2 the distribution is devoid of any well-marked feature. There is some evidence of a secondary maximum round about midnight.

For all Tipulinae, then, the peak of night activity is unquestionably attained in the early periods of the night—almost immediately after sunset. Taken as a whole there is then a gradual decrease in activity—interrupted by a slight secondary maximum just after midnight—throughout the rest of the night. The peak activity of the males is more evenly distributed over periods 1 and 2 than for the females, whose greatest abundance is quite definitely confined to period 1. This difference has been interpreted by Pinchin & Anderson as an "earlier flight of females". It seems more likely that both sexes attain maximum activity at much the same time, and that the males remain active for rather longer than do the females.

Taking the separate species, without exception greatest abundance is realized in one of the first two periods—in the majority of cases in the former of the two. Moreover a secondary maximum of activity is almost invariably attained later in the night—usually just after midnight. The only notable exception is *T. paludosa*, in which alone is observed a complete absence of any peak near midnight, coupled with a marked secondary maximum just before dawn. The "dawn maximum" of activity observed in the diagram for all Tipulinae is therefore entirely attributable to this one species, and in fact to the male sex of the species.

5. Influence of temperature on nocturnal activity

On the figures for two years Pinchin & Anderson were able to conduct a preliminary analysis of the effect of maximum and minimum temperatures on the captures of Tipulinae. A further two years' figures, in addition to verifying their conclusions, makes it possible to investigate the influence of temperature in much greater detail. By reason of its invariable abundance throughout the month of September, *T. paludosa* lends itself particularly to a detailed analysis of temperature effects. Consequently most of the following results are based on this species and this one month. Evidence has been obtained, however, by studying the effects of temperature on *T. paludosa* in August (when it is much less abundant than in September), and on *T. obsoleta* in the month of October, which definitely indicates that conclusions based on the captures of *T. paludosa* in its most active month can be applied to the sub-family as a whole. The further fact that in *T. paludosa* the predominant sex is the male whereas the female is the more active sex in *T. obsoleta* supports the above contention. No other single species was captured in numbers large enough to allow of similar statistical treatment.

(a) *Minimum and maximum temperature*

To study the influence of minimum temperature on the captures of *T. paludosa* two series of values were correlated (Table 3):

(1) Departures of the log catch of the species from a 15-day running mean.

(2) Departures of minimum temperature from a similar mean.

Table 3

Relation with minimum temperature

Species	Month	Correlation	Partial correlation	Regression	Partial regression
1933					
T. paludosa	**Sept.**	**0·77**	**0·75**	**0·082**	**0·087**
,,	Aug.	0·48	0·35	0·043	0·035
T. obsoleta	Oct.	0·76	0·57	0·059	0·054
1934					
T. paludosa	**Sept.**	**0·77**	**0·67**	**0·076**	**0·066**
,,	Aug.	0·55	0·19	0·034	0·012
T. obsoleta	Oct.	0·23	0·35	0·016	0·026
1935					
T. paludosa	**Sept.**	**0·62**	**0·24**	**0·055**	**0·022**
,,	Aug.	0·52	0·40	0·045	0·039
T. obsoleta	Oct.	0·41	0·26	0·027	0·024
1936					
T. paludosa	**Sept.**	**0·71**	**0·70**	**0·098**	**0·103**
,,	Aug.	0·57	0·48	0·049	0·049
T. obsoleta	Oct.	0·57	0·64	0·056	0·070
1933–6					
T. paludosa	**Sept.**	**0·72**	**0·64**	**0·075**	**0·071**
,,	Aug.	0·52	0·42	0·042	0·033
T. obsoleta	Oct.	0·50	0·48	0·037	0·046
		Relation with maximum temperature			
1933					
T. paludosa	**Sept.**	**0·25**	**−0·15**	**0·030**	**−0·013**
,,	Aug.	0·37	0·13	0·023	0·009
T. obsoleta	Oct.	0·62	0·08	0·081	0·011
1934					
T. paludosa	**Sept.**	**0·56**	**0·21**	**0·063**	**0·019**
,,	Aug.	0·63	0·41	0·043	0·033
T. obsoleta	Oct.	−0·10	−0·17	−0·008	−0·022
1935					
T. paludosa	**Sept.**	**0·78**	**0·64**	**0·094**	**0·075**
,,	Aug.	0·38	0·12	0·025	0·008
T. obsoleta	Oct.	0·33	0·04	0·037	0·006
1936					
T. paludosa	**Sept.**	**0·20**	**−0·12**	**0·031**	**−0·014**
,,	Aug.	0·05	−0·12	0·003	−0·001
T. obsoleta	Oct.	−0·03	−0·37	−0·014	−0·040
1933–6					
T. paludosa	**Sept.**	**0·43**	**0·094**	**0·054**	**0·010**
,,	Aug.	0·35	0·11	0·023	0·014
T. obsoleta	Oct.	0·21	−0·16	0·023	−0·019

In every year the value of the correlation coefficient was found to be positive and significant, varying between 0·77 in 1933 and 0·62 in 1935 (Table 3, heavy type). A similar correlation for each year with maximum temperature gave values which in two years were significant and in two years were not. The correlation for the four years combined was just significant at the 2% level. It is evident therefore that whereas minimum temperature invariably plays a significant part in determining the size of catch of *T. paludosa*, the effect of maximum temperature is not nearly so important. These facts are brought out more clearly when partial correlation coefficients are considered. When the influence of maximum temperature has been eliminated, the partial correlation with minimum temperature (0·64) is only slightly less

than the "total" correlation value (0·72), and is still on the four years' working well above the 2% level of positive significance. The partial correlation with maximum temperature, on the other hand, is negative in two years out of four and far from being significant (0·094) over the whole period.

Only in 1935 is the partial correlation with minimum temperature non-significant. This year too is the only one in which the partial correlation with maximum temperature is significant. In 1935 the mean minimum temperature for September was considerably lower than in the other three years, 48·9 as compared with 51·5, 50·2 and 51·7. It therefore seems probable that the influence of maximum temperature is only appreciable when minimum temperature is low. In support of this conclusion it is observed that the correlation with maximum temperature is approximately inversely proportional to the value of the mean minimum temperature. A correlation between the two series of values gives a figure of −0·9987 which is significant at the 1% level.

A consideration of regression coefficients again illustrates the overwhelming influence of minimum temperature. The four-year regression and partial regression on minimum temperature are respectively 0·075 and 0·071, as compared with 0·054 and 0·010, the corresponding figures for maximum temperature. The reduction in value, by taking a partial regression, is again slight in the first instance and large in the second. The regression and partial regression on minimum temperature mean that an increase in the log catch of 0·30 (equivalent to a doubling of the numerical catch) is brought about on an average by a rise of 4–4½° F. in minimum temperature. Whereas, on a partial regression of 0·010, the increase in maximum temperature required to double the catch would be more than 30° F. As this latter partial regression is not significant and is made up of two negative and two positive values it is not possible to determine how much more important is minimum than maximum temperature.

Correlations with minimum and maximum temperatures, using actual numbers instead of logarithms, give very similar results (Table 4). The figures show a slight general reduction on the former values, but for the four years the partial correlation with minimum temperature is always significant,

Table 4. *Numerical catches of* Tipula paludosa *in September*

T. paludosa	September	Correlation	Partial correlation	Regression
Related to minimum temperature	1933	0·68	0·60	3·62
	1934	0·66	0·48	1·87
	1935	0·64	0·42	0·80
	1936	0·57	0·59	2·04
	1933–6	0·59	0·53	2·03
Related to maximum temperature	1933	0·18	−0·29	1·10
	1934	0·59	0·34	1·92
	1935	0·58	0·29	1·08
	1936	0·08	−0·20	0·33
	1933–6	0·30	−0·004	1·26

that with maximum temperature is never significant and on an average the latter is negative. One interesting difference observed when numbers are used is that neither correlation nor partial correlation with maximum temperature is ever greater than the corresponding figure with minimum temperature. In this respect numbers give a slightly greater consistency than logarithms, but when regressions on the two systems are calculated the advantage of using logarithms becomes markedly apparent. For example, the numerical regression on minimum temperature varies between 0·80 and 3·62, depending very largely on the total abundance of the species in the year concerned. The variability of the corresponding regressions on the logarithm basis is, in comparison, very small—extreme values being 0·055 and 0·098—and is independent of numerical abundance. These figures indicate quite clearly that, as would be expected, the catch of *T. paludosa* increases with temperature in a geometric rather than in an arithmetic ratio. Herein, then, lies a very strong argument for the use of the logarithmic system.

Statistical analysis of the relation between catches of *T. paludosa* in August and of *T. obsoleta* in October, and maximum and minimum temperature, affords striking corroboration of the above conclusions. For *T. paludosa* (Table 3) the correlation with minimum temperature is again always positive and always significant. The values, however, are not quite so high as they are in September, due to a larger number of zero captures which always reduce the correlation. Likewise the regression, again noticeably consistent, shows that in August when the species has not attained maximum activity, the increase in minimum temperature required to double the catch is in the neighbourhood of 7° F.—considerably higher than in September. For *T. obsoleta* (Table 3) the relationships are substantially similar. Once more the correlation and partial correlation with minimum temperature are positive and in general significant. With maximum temperature they are again non-significant, the partial correlation being negative. The partial regression on minimum temperature, value 0·046, indicates a similar average increase of about 7° F. as being necessary to double the catch of *T. obsoleta*.

(*b*) *Daily range of temperature*

A study of the relation between catch of *T. paludosa* and difference between maximum and minimum temperature (daily range), indicates a further significant relationship. For these calculations departures from 15-day running means were again used, since there is a progressive shortening of the daily temperature range throughout the month of September. The values of correlations and regressions were found invariably to be negative, and significant in three years out of four. For the four years combined a correlation coefficient of $-0·45$ is definitely significant. It appears therefore that a small daily range in temperature is favourable to a large capture of this species. This conclusion is confirmed by the often observed fact that on a clear night—when there is

always a rapid fall in temperature—the conditions are unfavourable for insect activity. The four-year regression figure of $-0{\cdot}052$ indicates that a reduction of about 6° F. in the daily range of temperature will effect a doubling of the catch of *T. paludosa* in its month of greatest activity (Table 5).

Table 5. Tipula paludosa *and difference between maximum and minimum temperatures* (*daily range*)

September	Correlation	Regression
1933	−0·54	−0·058
1934	−0·36	−0·041
1935	−0·16	−0·019
1936	−0·68	−0·094
1933–6	−0·45	−0·052

Catch is doubled by a reduction of approximately 6° F. in daily range.

This significant relationship with daily temperature range may actually be deduced from the nature of the relationships with maximum and minimum temperature. From the facts of a significant correlation with minimum temperatures and a non-significant relationship with maximum temperature it follows that there will be a significant correlation with the difference between the two. The value of the latter correlation coefficient can, however, only be determined by relating directly the two series of values—insect catch and temperature range. Remembering that no corrections have been made for any other factors which are known to affect activity, e.g. wind, cloud, moonlight, it still seems evident that temperature plays a very important part in determining variations in the catch of Tipulinae (as exemplified by *T. paludosa* and *T. obsoleta*) within a single year. Correlations between all Tipulinae and minimum temperature throughout the six summer months gave coefficients of 0·46 and 0·55 respectively in 1935 and 1936. Since each of these figures is based on about 170 observations their significance is high.

Minimum temperature is then unquestionably the more important single thermal factor in determining activity in Tipulinae. By comparison, maximum temperature has relatively little effect on the abundance of the group. Only when the minimum temperature is low, and its influence reduced, does the effect of maximum temperature become apparent. Additional evidence for this last conclusion is found in the observation that the correlation with maximum temperature is very roughly inversely proportional to that with minimum temperature.

The activity of Tipulinae is therefore: (1) very definitely favoured by a high minimum temperature, (2) definitely favoured by a small difference between maximum and minimum temperature, (3) little affected by changes in maximum temperature at least in so far as these are independent of minimum temperature.

6. Influence of cloud and moonlight on activity

In dealing with the influence of cloud and moonlight on the captures of all Tipulinae, the system devised by Dr C. B. Williams (1936) has been adopted. This system differentiates nine different combinations of conditions of cloudiness and moonlight. The nights of the six summer lunar months are divided into: (1) nights in the full-moon weeks; nights in the no-moon weeks; and nights in intermediate weeks; (2) nights of less than 10% cloud; 10–90% cloud; and more than 90% cloud. The nine possible combinations of the above two series are then set out in a square diagram as illustrated in Table 6.

Table 6. *All Tipulinae. Percentage of mean catch*

		Clear	Intermediate	Cloudy	
Full moon	1933	53	49	150	63
	1934	15	129	107	59
	1935	39	78	87	70
	1936	10	60	128	54
	1933–6	**31**	**69**	**111**	**63**
Intermediate	1933	66	72	274	107
	1934	68	162	68	111
	1935	68	118	109	97
	1936	46	85	190	106
	1933–6	**63**	**104**	**160**	**103**
No moon	1933	54	183	234	133
	1934	88	184	231	161
	1935	57	141	341	156
	1936	49	135	281	134
	1933–6	**60**	**163**	**265**	**142**
	1933	59	87	239	
	1934	51	152	114	
	1935	59	109	154	
	1936	36	88	186	
	1933–6	**53**	**106**	**166**	

These figures have been calculated in a series of steps. In the first place the actual log catch of all Tipulinae for each night in the six summer lunar months is placed in the appropriate square of the diagram, according to the prevailing conditions of moonlight and cloud. The mean log catch for each category is then calculated. These mean log catches are reconverted into numbers by taking the antilogarithm in each case and subtracting unity. And finally each of these numbers is expressed as a percentage of the mean catch for the whole period concerned, whether it be one summer or four summers combined, calculated in the same way by reconversion of the appropriate mean logarithm.

The minimum catch, approximately one-third of the mean, is recorded on clear nights of the full-moon weeks, whereas the maximum catch of more than two and a half times the mean occurs in cloudy nights in the weeks of no moon. Expressing this result in another way, the activity of Tipulinae under the most favourable conditions of cloud and moonlight is some eight or nine times as great as that attained in the least favourable circumstances. Between these two extremes there is a consistent rise in catch from full-moon periods to no-moon periods and from clear nights to cloudy nights.

On the right-hand side and bottom of the table are figures summarizing respectively the influence of moonlight irrespective of cloud, and the influence of cloud independent of moon. Between nights of full moon and nights of no moon the difference in percentage of mean catch is 79: between clear nights and cloudy nights it is 113. It therefore appears that both cloudiness and moonlight have marked effects on the captures of Tipulinae, but that the influence of cloud is about one and a half times as great as that of moonlight.

In the preceding table no account has been taken of fluctuations in minimum temperature. Table 7 shows that the minimum temperature varies considerably with prevailing conditions of cloud, but is unaffected by varying phases of the moon. On an average for the four years the minimum temperature was 1·88° below the normal on clear nights and 2·18° above normal on cloudy nights. The mean minimum temperature on a clear night was therefore almost exactly 4° F. below that of a cloudy night. In view of the importance of minimum temperature in determining activity of Tipulinae it seemed likely that this temperature difference must largely, if not entirely account for the observed difference between catches on clear and cloudy nights. Accordingly the figures were adjusted statistically to exclude the influence of minimum temperature. When all pure temperature effect had been eliminated the resulting difference between clear and cloudy night captures was found to be positive but non-significant. Though there remained some evidence of an independent cloud effect, in that catches over the four-year period were still slightly lower on clear than on cloudy nights, it appears that on the whole the observed influence of cloud conditions on the activity of Tipulinae may be almost entirely attributed to related variation in minimum temperature.

Table 7. *Minimum temperature. Four-year summary of mean departures from monthly running means*

	Clear	Intermediate	Cloud	
Full moon	−1·50	−0·63	+1·88	−0·27
Intermediate	−2·06	−0·10	+2·14	−0·05
No moon	−1·93	+0·08	+2·52	+0·15
	−1·88	−0·18	+2·18	

For the four years involved the temperature on a night of no moon was on an average 0·42° F. higher than on a night of full moon. This result can only be regarded as accidental, since there is obviously no relation between minimum temperature and the phase of the moon. The accidental nature of the final figure is borne out by observation of the separate yearly figures. The warmest nights in the four years are quite independently arranged in the various categories of moonlight, falling once in the full-moon period, once in the intermediate, and twice in the no-moon period.

The effects of moonlight and cloud on the activity of Tipulinae are therefore: (1) Both factors have a marked influence. (2) Optimum conditions are complete cloudiness and no moon. (3) Least favourable conditions are complete

absence of cloud and a full moon. (4) Between these extremes there is a consistent increase in catch with decrease of moonlight and increase of cloud. (5) The catch under optimum conditions is some eight or nine times as great as when conditions are least favourable. (6) The effect of cloud, almost all of which may be attributed to the related minimum temperature, is to treble the catch of a clear night. (7) The catch on a night of no moon is rather more than twice that on a moonlight night.

7. SUMMARY

1. The total number of crane-flies of the sub-family Tipulinae captured in a light trap at Rothamsted Experimental Station in the four years 1933–6 was 3394. This number comprises seventeen species, seven of which were comparatively numerous in each of the four years. By far the most common single species is *Tipula paludosa*, accounting for 57·4 % of the total capture. The ten "rare" species accounted for no more than 1 % of the total.

2. *Sex proportions* show that in general males are attracted to light in larger numbers than are females: the former comprise 65·4 % of the total catch. Species in which males predominate are *Tipula paludosa*, *Pales flavescens*, *P. maculata* and *Tipula pagana*. (In the last-named species the females are wingless.) Species in which females predominate are *Tipula marmorata*, *T. obsoleta* and *T. oleracea*.

3. *Monthly distribution.* Greatest activity for the group as a whole is recorded in September and is due to *T. paludosa*. A minor peak occurs in June as a result of the activity of *P. flavescens*. July is throughout a month of reduced activity. It is probable that *T. oleracea* alone is definitely double-brooded, and that *T. paludosa* may also have two broods in the year; but the other five species are clearly single-brooded.

Species	Mean period of activity	Length of period days	Time of maximum activity
T. oleracea	20 May – 4 Oct.	137	Brood I, mid-May to end of June Brood II, mid-Aug. to end of Sept.
P. maculata	13 May –27 June	45	Latter half of May
P. flavescens	11 June– 2 Aug.	52	Latter half of June
T. paludosa	2 July –19 Oct.	109	Middle of Sept.
T. marmorata	18 Sept.–20 Oct.	32	End of Sept.
T. obsoleta	28 Sept.–28 Oct.	30	Middle of Oct.
T. pagana	9 Oct. – 4 Nov.	26	About 21 Oct.

4. *Night distribution.* Activity of Tipulinae is invariably greatest just after sunset, and is maintained at a maximum slightly longer in males than in females. A gradual decrease in activity after the sunset maximum is interrupted by a slight secondary maximum near midnight and then continues until sunrise. The only exception to this generalization is *T. paludosa* which shows no maximum at midnight and a definite rise in activity towards dawn. The activity of males follows the general trend for the group more closely than that of females. For the separate species examined the primary maximum

invariably occurs in the first quarter of the night, and there is almost invariably a secondary maximum, usually just after midnight.

5. *Influence of temperature* was investigated by means of correlations and regressions, both total and partial, with maximum and minimum temperature. The influence of daily range in temperature was also examined. From this study the following conclusions emerge: (1) activity is very definitely favoured by a high minimum temperature; (2) activity is definitely favoured by a small difference between maximum and minimum temperatures—daily range; (3) activity is little affected by changes in maximum temperature, at least in so far as these are independent of minimum temperature.

At the time of greatest activity of the group it appears that a rise of 4–4½° F. in the minimum temperature will effect a doubling of the catch. The same result is produced by a reduction in the daily range of temperature of some 6° F.

6. *Influence of cloud and moonlight.* Both factors have a marked effect on the captures of Tipulinae. Optimum conditions are absence of moonlight and complete cloudiness. The converse conditions of full moon and no cloud are the least favourable to activity. Between these extremes there is a consistent increase in catch with increasing absence of moon and presence of cloud. The catch under optimum conditions is eight or nine times as large as in the least favourable circumstances. On a night of no moon the insects are rather more than twice as numerous as on a night of full moon. The effect of cloud, almost all of which may be attributed to the related minimum temperature is to treble the catch of a clear night.

8. Acknowledgements

The writer wishes to record his gratitude to Dr C. B. Williams for his advice and assistance throughout the course of this work. His thanks are also due to Dr F. W. Edwards of the British Museum (Natural History) for assistance in identification of the rarer species, and to Mr W. G. Cochran of the Rothamsted Statistical Department for advice on the statistical investigations involved.

References

Pinchin, R. D. & Anderson, J. (1936). "On the nocturnal activity of Tipulinae (Diptera) as measured by a light trap. Proc. R. Ent. Soc. Lond. A, 11: 69–78.

Williams, C. B. (1935). "The times of activity of certain nocturnal insects, chiefly Lepidoptera, as indicated by a light-trap." Trans. R. Ent. Soc. Lond. 83: 523–55.

Williams, C. B. (1936). "The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap." Philos. Trans. B, 226: 357–89.

Williams, C. B. (1937). "The use of logarithms in the interpretation of certain entomological problems." Ann. Appl. Biol. 24: 404–14.

Keys

Audcent, H. [L. F.] (1932). "British Tipulinae (Diptera, Tipulidae)." Trans. Ent. Soc. S. Engl. 8: 1–34.

Pierre, C. (1924). "Diptères: Tipulidae." Faune de France, 8: 1–159. Paris.

A POPULATION STUDY OF SUBTERRANEAN SOIL COLLEMBOLA

By J. P. GLASGOW

Imperial College of Science and Technology, Biological Field Station, Slough

(*With* 5 *Figures in the Text*)

CONTENTS

		PAGE
1.	Introduction	323
2.	Acknowledgements	325
3.	Sampling	325
4.	Technique	327
5.	Horizontal distribution	328
6.	Choice of sample size	333
7.	Vertical distribution	335
8.	Population fluctuations	338
9.	Summary	344
	Appendix 1. Census counts	345
	Appendix 2. A simple soil sampler	352
	References	353

1. Introduction

It is well known that large numbers of different species of animals are found in the soil. At Rothamsted, Baweja (1939), found 275 different species in the soil fauna, while Frenzel (1936) found a total of 422 in various parts of Germany. In the present study no attempt was made to identify all the forms found. Attention has been concentrated on that part of the fauna which is truly subterranean. The majority of the animals commonly designated "soil" belong in fact to the surface or sub-surface. Though they may be found at considerable depths in arable land, in the more stable environment of the meadow they keep to the top. They are active animals, with body pigment and eyes, and they live in that ill-defined region where stem merges into root, where the plant covering protects delicate forms from climatic extremes, but daylight penetrates and there is more vegetation present than actual soil.

Below this there is a region of perpetual darkness, inhabited by a community of sluggish white blind animals whose modifications recall those of the cave fauna. Some are in fact recorded as cave forms (*Onychiurus armatus*, *O. ambulans*, *Tullbergia krausbaueri*). In the area under consideration this "truly subterranean" fauna consists of Symphyla, four species of Onychiuridae, and occasional specimens of the Achorutid *Anurida granaria*.

Pauropods and Protura are also found sometimes. Chilopods, the larvae of Elateridae and other beetles, larvae of Tipulidae and other flies, and earthworms, are also encountered deep in the soil. These animals, however, are of a different order of size from the Onychiuridae, and apart from the earthworms, are normally concentrated near the surface.

The relationship between the large animals and the Onychiuridae is obscure. It has been conjectured that Collembola and mites perform in the economy of the soil a role analogous to that of the animal micro-plankton of the soil—themselves herbivorous, being preyed on by larger carnivores. But this attractive proposition lacks concrete demonstration, and it is not impossible that the larger animals are in fact quite independent of the smaller. The present investigation can contribute nothing in this direction, for the study of, for examples, wireworms, has been shown by Jones (1937) to require samples as large as 1 sq. ft., which is impossibly big for Collembola investigations.

The present study is concerned with the Onychiuridae, of which four species were present—*Onychiurus armatus* Tullb., *O. ambulans* Nic., *Tullbergia quadrispina* Börner and *T. krausbaueri* Börner. These are all shining white naked animals, with short legs and no springing apparatus. The antennae, though short, are very sensitive and quiver continuously while the animals are walking. Digging is impossible for these soft feeble beasts, and they move only through the pores of the soil. Ford (1935) has shown that they are exterminated when the soil is made non-porous. *O. armatus* is a cosmopolitan species. Handschin gives for its habitats: under stones, in earth, and under bark. Frenzel regards it as a permanent inhabitant of meadow soil and a "Leitform" (one tolerating a wide range of habitats). In the United States it is a minor pest of sugar-cane (Spencer & Stracener, 1930; Ingram, 1931). Strebel (1932) found it very sensitive to sudden strong light, but as Cameron (1917) noticed in *O. ambulans*, none of the Slough Onychiuridae appear to avoid steady light. *O. ambulans* lives in earth, under stones and bark, and in caves (Handschin). Though widely distributed, it is more restricted than *O. armatus*. Frenzel did not find it in any of his meadows, but at Slough it is the most abundant species present. Ripper (1930) records it from mushroom beds. *Tullbergia quadrispina* occurs under stones and in humous soil (Handschin). Frenzel found it in three of his eight meadows, and notes that it is particularly deep-living. *T. krausbaueri* is much smaller than the other three species. They vary from 1 to 2·5 mm. in length, but *T. krausbaueri* does not exceed 1 mm. Handschin records it from humus, hot-houses, under flower-pots and under the damp bark of trees, in caves and on mushrooms. It is one of Frenzel's Leitformen, occurring in six of his meadows.

There is little information available on the life history of Onychiuridae. The most nearly related animal for which there is exact information is *Hypogastrura manubrialis* Tullb. The Hypogastruridae belong to the same superfamily, Poduromorpha, as the Onychiuridae. *H. manubrialis* has

attracted attention because it is a pest of mushroom beds, in which habitat it is sometimes accompanied by *O. ambulans* and *T. krausbaueri*. Its life history is summarized by Ripper (1930) as follows: the egg hatches in 19 days at 22° C., in 36 days at 10° C.

1st moult	7 days old
2nd moult	15 days old
3rd moult	22 days old
Sexual maturity ...	5–7 weeks
Total life-span ...	5–10 months

Moulting goes on throughout life, even after sexual maturity. Strebel (1932) gives similar figures for *H. purpurascens*. It would be extremely rash to assume that these figures are at all closely applicable to Onychiuridae, but they are the best information available and do show the type of life history which it is reasonable to expect.

2. Acknowledgements

This work has been done under the general direction of Prof. J. W. Munro. I am greatly indebted to Dr O. W. Richards, who supervised the work at every stage; and to Prof. F. G. Gregory, of the Plant Physiology Department of this College, who gave statistical advice and in particular devised the experiment on horizontal distribution. The late Dr W. Maldwyn Davies gave invaluable help, in the early stages, with the identification of Collembola.

3. Sampling

Sampling was carried out in the Pond Field at the Biological Field Station, Slough. This field had not been cultivated for at least ten years, and quite probably not for twenty, the only attention it received being annual hay-making. It is covered with coarse grass, cocksfoot (*Dactylis glomerata*) being very common. Couch grass (*Agropyrum repens*) is also present, as well as timothy grass (*Alopecurus pratensis*) and dock (*Rumex* spp.). There is a good deal of moss among the grass and other plants. The south side of the Pond Field is bounded by a stream, and the west side by a ditch which usually contains water only 2 or 3 ft. below the surface of the field. In a wet winter the water table rises almost to the surface.

As already mentioned, no attempt has been made to compile a complete list of the soil fauna, but some mention must be made of its more important characteristics. In numbers of individuals, Collembola comprised about 80% of the total fauna. Mites (Acarina) and Myriapods were of approximately equal abundance, the mites being concentrated at the surface, while the Symphyla (the most numerous Myriapods) are truly subterranean. Other Myriapods regularly present included Chilopods, both Lithobiidae and

Geophilidae, Diplopods and Pauropods. Larvae of Elateridae (Coleoptera), probably *Agriotes obscurus* Linn., were present in every sample, the numbers ranging from 3 to 33 per sample of 628 cu. in. (10·6 litres). Sometimes the larvae of crane-flies, *Tipula paludosa* Meig., occurred. The ant *Myrmica ruginodis* Nyl. occurred fairly regularly, and on one occasion (20 Sept. 1937) there were 95 in a single boring of 1180 c.c. The remainder of the fauna was composed of sporadically occurring animals such as the larvae of various Coleoptera and Diptera, nymphs of Hemiptera, thrips, spiders and earthworms.

In a patch of the Pond Field 80 × 50 ft. (24 × 15 m.) nine plots were marked out in a modified latin square. The three large plots SW, NC, EC, each 25 × 15 ft., were left quite undisturbed except that they were mowed twice each summer when the grass got inconveniently long, and it is with the samples taken from these plots alone that the present paper is concerned.

A sample consisted of 9 borings, 3 from each plot. Each plot was divided into imaginary 1 ft. squares, which were numbered consecutively. To determine the position of the borings, numbers were drawn at random from a box, a special box of numbers being kept for each plot. From a diagram was found the latitude and longitude of the centres of the squares so chosen, and the exact place to bore was then measured out on the plot and marked with a peg. This method ensured that the borings were placed at random, and that no boring could be less than a foot from the site of any previous boring. After the sampling, the holes were filled up with gravel.

The ideal size of a soil sample is closely bound up with the distribution in the soil of the various species being studied. Consideration of this matter is therefore deferred until after Section 5 on "Horizontal distribution".

The three borings from each plot were not washed separately, but mixed and passed through the machine together. More information would have been obtained had each boring been dealt with separately, but with the form of apparatus used this method would have been too laborious. The soil was a heavy clay containing very few stones. At about 13 in. a blue layer was encountered. The pH by Wulff strip-colorimeter method was $5{\cdot}0 \pm 0{\cdot}2$. A few simple constants were determined for the various layers:

	Ignition loss (%)	Moisture in air-dry soil (%)	Moisture in saturated soil (%)
4·5 in. (11·4 cm.)	14·05	5·944	96
4·5–9 in. (11·4–22·9 cm.)	10·78	5·942	58
9–13·5 in. (22·9–34·3 cm.)	9·82	7·650	58
13·5–16 in. (34·3–40·6 cm.)	8·37	6·040	—

The percentages refer to the dry weight of the soil. The estimate of the saturated moisture is only rough, and is derived partly from laboratory measurements by the rim method, which tries to use the soil undisturbed in the condition it was in in the field, and partly from soil-moisture determinations when the soil was water-logged. The top layer was very variable in this respect;

the rim, which is about an inch deep, pressed into the surface of the soil, has given values as high as 130%.

Ground temperatures at 75 cm., 25 cm. and 10 cm. are taken at 09.00 every morning at the Field Station. In October 1936 the 10 cm. readings were replaced by a distant recording thermograph with the sensitive bulb at 10 cm. All these temperatures were taken not on the sampling plots but some distance away, under short turf.

4. TECHNIQUE

While many methods of separating insects from soil have been described, the flotation method of Ladell (1936) is for small animals so far superior to other methods that results obtained with it can be compared only with great caution to those obtained in other ways. A large Ladell's apparatus, considerably modified, was used. The mixing cylinder held 60 litres instead of 15, and the apparatus could take a 9-in. (23 cm.) cube (30–40 lb.) of soil at once. The size involved some modifications. A much stronger air current was used, and the turbulence induced by this was responsible for most of the stirring. A continuous mechanical stirrer was dispensed with, as occasional hand stirring was found to be sufficient. After passing across a settling tank the yield was caught in a Buchner funnel on a piece of 200 mesh Monel wire gauze. This holds animals just visible to the naked eye, but is very much quicker than filter paper and obviates the use of a suction pump.

It was a mistake to make such a big apparatus. It was begun because of a statement by Thompson (1924) that a 9-in. cube was a proper size for a soil sample. At that time I did not realize the advantages to be gained by subdividing and taking a composite sample composed of a number of smaller scattered ones. Actually the machine was scarcely ever used to capacity. In the ordinary way the size of a sample was 108 cu. in., which is exactly the size that Baweja regularly put into Ladell's original apparatus. Thus the greater capacity of my apparatus was unnecessary, while it was heavier to work and not so quick.

The product of these machines is a large quantity of vegetable debris in which the soil animals are entangled and from which they can be separated only by laborious hand sorting. The debris was washed off the wire gauze filter into a green photographic developing dish. This had a narrow level spout which came comfortably into the field of a binocular microscope with a magnification of $\times 140$. The debris was dragged into the spout with stout needles, vegetable matter allowed to fall and animals transferred to a watch-glass of 70% alcohol. This method seems superior to that of examining on the filter in strips or squares, as it is continuous and there is no need to stop searching in order to move the container. The separation of the animals from the vegetable debris is the longest and most tedious part of the process of

taking a soil sample, and one of the factors limiting the total amount of soil which can be examined. To bring a normal sample of 972 cu. in. (40–50 lb.) in from the field, wash it and sort it, usually took 4 days.

A second and in this case more important factor limiting the number of samples taken is the time taken to identify and count the animals. In previous soil studies large numbers of species have been identified and recorded as present, but the numbers of individuals of each species have not been recorded. The discussions of populations have referred to larger units such as families or orders. The distinction is important, because the identification of large numbers of Collembola, particularly, consumes a great deal of time. A certain number of specimens are bound to get damaged, and even when I had been identifying Onychiuridae for 18 months I sometimes found it necessary to use a magnification of 500 diameters to determine a damaged *Onychiurus*. The last sample taken on 16 October 1937 contained 1521 Onychiuridae, 694 other Collembola, 595 other animals. After the animals had been separated from the debris and brought into alcohol, to sort and count them and identify the Onychiuridae took 21 working hours. This was a fairly small sample and my speed was then much greater than it was earlier on. The sample taken on 16 September 1936, for example, contained 1230 Onychiuridae, 395 other Collembola, 948 other animals, and sorting, counting and identification occupied 35½ working hours. At times much larger samples had to be dealt with. Some of the Onychiuridae could be identified with binoculars as they lay in the alcohol, but most had to be transferred to lactic acid. After being cleared, the majority could be identified under a high power binocular, but a few had to be temporarily mounted on a cavity slide and examined with a monocular.

Each boring had an area of 8 sq. in. (52 sq. cm.). Early samples were taken to a depth of 9 in. (22·9 cm.), later samples to 13½ in. (34·3 cm.) and a few to 16 in. (40·6 cm.). A sample was composed of nine such borings, and all but three of the samples were divided into 4½ in. layers, for investigation of the vertical distribution of the fauna.

5. Horizontal distribution

Recent work of Blackman (1935), Ashby (1935) and others has drawn attention to the problem of the distribution of species in plant associations. Though a number of methods of describing plant associations have been developed which are based on the assumption that individuals of a species are distributed at random within the bounds of an association, it now appears that many species are not so distributed. Some are under-dispersed, that is, they tend to occur in groups or clumps; while others are over-dispersed: their distribution is more regular than a random distribution. In other words, an under-dispersed species tends to occur in aggregations, members of a randomly

dispersed species are indifferent to one another, but members of an over-dispersed species tend to be widely spaced in relation to their frequency.

The distribution of sessile and sedentary animals such as soil animals can be thought of in the same way as the distribution of plants, but the problem has attracted little attention. Jones (1937) in Washington found that some wireworms are distributed at random. Probably his populations of "wireworms" are composed of several different species, about whose distribution there is no information. Thompson (1924) performed an experiment which has since been taken to show (*a*) that the soil fauna is uniformly distributed (Ford, 1937 *b*), (*b*) that a 9-in. cube is a satisfactory soil sample. The experiment consisted in counting the "Achorutidae" (a group including Onychiuridae, possibly equivalent to Poduromorpha) present in several series of samples, each of twenty 2-in. cubes. In some cases these were taken more or less at random, though similar vegetative coverings were selected for the sampling positions, in others they were taken along definite lines. The totals of these various series agreed closely, though the individual counts showed a wide range. From this it was concluded that a 9-in. cube, having the same area as twenty 2-in. cubes, "might be expected to give a reasonable picture of the Achorutid population of the soil as a whole, and that such a sample was a reasonable one on which to work in attempting to trace quantitatively the seasonal changes of the fauna".

This conclusion will not win support from anyone used to more modern statistical methods. It assumes that the variance over a whole field with an area of some 2000 sq. ft. will be no greater than that over 81 sq. in. But the fact that the numbers present in the small sampling units showed a great range is direct evidence that this is not so. Thompson's evidence shows that a sample of twenty scattered 2-in. cubes might be considered satisfactory, but not at all that one 9-in. cube would be satisfactory. Moreover, the distribution of the "Achorutidae" throws little light on the distribution of its constituent species, and none at all on that of other soil animals.

In the present investigation, it was unfortunate, from the point of view of the study of distribution, that the three borings taken from each plot in a routine sample were mixed together. Had separate counts from each boring been available, it would have been possible to test the distribution by means of the Poisson series. But as this was impossible, a special experiment was devised. This was a sample consisting of nine pairs of borings, three pairs at random on each plot, and the members of a pair touching. Then, in a species distributed at random in the soil, the number of individuals present in one member of a pair of borings should be independent of the number in the other. If on the other hand the species is under-dispersed, in aggregations, the two counts from a pair of borings should be correlated, while in an over-dispersed species they should be negatively correlated.

The first experiment on the distribution of the animals was made on

11 November 1936. The two members of a pair of borings were taken in quick succession, the first hole being stopped with a cylinder of a size to prevent the wall crumbling. The borings were taken to 9 in. only, and not divided into layers as usual. The following counts are given in their plots, and the two members of a pair are designated West and East respectively.

When the variance of this material is analysed, it is found that in each of the four species the variance between pairs was significantly greater than the variance within pairs. In other words, all four species occur in aggregates. The result is highly significant, exceeding the 0·001 level of significance in every case except that of *T. quadrispina*, in which case P is 0·05–0·01. The four species considered together are also aggregated, P 0·05–0·01. The moisture and ignition loss appear to be distributed at random.

Having established that the animals occur in groups, it is of interest to know the size of the groups. In the last experiment the centres of the borings were 3 in. apart (the diameter of the borer) so that the size of the aggregations must be of at least this order. Repetition of the experiment with the members of each pair increasingly far apart should discover the upper limit of size of the aggregations, for if the members of a pair are taken a distance apart much greater than the size of the aggregations, the aggregations will not be detected and the animals will appear to be distributed at random. The experiment was accordingly repeated on 20 September 1937, taking the members of each pair 1 ft. apart.

Here, in the case of *O. armatus* there is no difference in variance within pairs and between pairs. In the case of the other three species there is a significant difference, which for *O. ambulans* P is less than 0·001, for *T. quadrispina* and *T. krausbaueri* P is 0·01–0·001. For the last three species considered together the difference is very significant, P being less than 0·001, while for all four species considered together the difference is less significant, P 0·05–0·01. This means that if *O. armatus* is aggregated the aggregations are less than a foot in diameter, so that they are not detected by this experiment. But the other species are grouped in aggregations a foot or more across, while the moisture and that property measured by ignition loss lie in patches of the same order of size.

We may now enquire into possible causes of this irregular distribution. For each boring the moisture content, ignition loss and pH value were determined. These constants were selected because they are factors which might reasonably be expected to affect soil animals and are also easy to determine. They by no means exhaust the list of possible soil physical factors which may be important. The pH value was so constant that its influence was discounted. Correlation coefficients were calculated between the numbers of each of the four species and the measurements of each of the physical factors. This was done separately for the data in Table 1 and Table 2. In some cases the correlations on these two dates were very different, and it was thought that this might be due to the soil being very much wetter on the first occasion.

Confirmation of this supposition was sought from the routine samples. Of these there

Table 1. *Distribution of Onychiuridae on* 11 *November* 1936. *Members of random pairs touching*

	Onychiurus armatus		*Onychiurus ambulans*		*Tullbergia quadrispina*		*Tullbergia krausbaueri*		4-spp. total		Moisture		Ignition loss	
	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.
SW	34	61	17	21	37	53	14	13	102	148	48·73	54·00	15·48	13·52
	5	9	35	48	9	6	2	5	51	68	50·36	56·24	13·03	14·38
	17	13	148	114	18	7	7	9	190	143	50·84	52·37	12·18	11·94
NC	18	4	29	20	9	13	101	90	157	127	49·76	49·97	13·07	13·89
	32	16	37	10	20	5	21	7	110	38	54·01	45·26	12·72	11·65
	11	7	9	4	25	15	26	25	71	51	49·56	50·39	11·92	12·62
EC	29	18	78	107	13	20	19	38	139	183	55·56	50·28	12·59	13·57
	65	72	49	65	28	45	12	12	154	194	58·43	55·49	12·79	11·94
	12	3	109	62	36	21	36	46	193	132	54·98	52·61	8·46	11·75

Mean moisture 52·16 %, mean ignition loss 12·67 %

Table 2. *Distribution of Onychiuridae on* 20 *September* 1937. *Members of random pairs* 1 *ft. apart*

	Onychiurus armatus		*Onychiurus ambulans*		*Tullbergia quadrispina*		*Tullbergia krausbaueri*		4-spp. total		Moisture		Ignition loss	
	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.
SW	18	5	56	60	12	2	14	11	100	78	42·81	35·08	11·65	10·26
	13	15	37	46	2	8	10	7	62	76	34·06	42·66	9·98	12·25
	14	27	107	174	18	21	12	7	151	229	46·01	48·71	11·83	11·61
NC	11	12	28	25	19	17	7	23	65	77	34·15	33·86	10·47	12·47
	15	36	8	27	16	3	59	41	98	107	32·63	35·28	9·86	10·39
	18	32	5	2	44	69	21	24	88	127	31·77	30·65	12·30	11·48
EC	24	56	0	1	16	11	13	6	53	74	53·65	41·93	13·11	14·03
	13	7	35	26	16	4	21	13	86	50	42·85	41·26	14·41	13·25
	35	55	6	3	6	9	9	16	56	83	33·10	39·51	10·90	11·44

Mean moisture 39·53 %, mean ignition loss 12·06 %

were 23, for each of which counts were available from each of the three plots, together with moisture determinations and, in most cases, ignition losses. The raw data is given in the Appendix. For the whole series the mean moisture content was 47 %. In 10 samples the moisture content lay above the mean, and in 13 below. These two groups of routine samples were then treated separately as "drys" (13 samples, mean moisture content 38·97 %) and "wets" (10 samples, mean moisture content 52·16 %). To obtain correlation coefficients from the data given in each of Tables 1 and 2 no allowance need be made for fluctuations in populations at different times of the year. But when different dates are combined it is necessary to eliminate the effect of population fluctuations, if, as at present, we are concerned only with spatial distribution. To do this, the numbers of each species in any plot were expressed as a percentage of the total numbers of that species in all plots on that date, and this percentage was used to derive the correlations between numbers and the physical factors measured. These correlations therefore concern spatial distribution only and are not affected by population changes.

Partial correlations between percentage numbers of insects, percentage content and percentage ignition loss were separately calculated for the "wets" and the "drys". In most cases the differences between the wets and the drys confirmed the differences between the wet sample of 11 November 1936 and the dry sample of 20 September 1937. In the following table, the column P indicates the level of significance. Where no value of P is given the correlation is not significant (P exceeds 0·05).

Table 3. *Partial correlations—horizontal distribution*

	11 Nov. 1936 mean moisture 52·16%		Wets mean moisture 56·98%		20 Sept. 1937 mean moisture 39·53%		Drys mean moisture 38·97%	
		P		*P*		*P*		*P*
Moisture-ignition loss	−0·1446	—	0·2911	—	0·5930	0·02–0·01	0·4402	0·02–0·01
Onychiurus armatus-moisture	0·5335	0·05–0·02	0·5254	0·01	0·0174	—	−0·0410	—
Onychiurus armatus-ignition loss	0·2220	—	−0·1052	—	0·1171	—	0·0938	—
Onychiurus ambulans-moisture	0·2748	—	0·2767	—	0·5504	0·05–0·02	0·5059	0·01
Onychiurus ambulans-ignition loss	−0·3733	—	0·0109	—	−0·3579	—	−0·3047	—
Tullbergia quadrispina-moisture	0·3310	—	−0·1612	—	−0·3926	—	0·6418	0·01
Tullbergia quadrispina-ignition loss	−0·0327	—	0·1440	—	0·3245	—	−0·5586	0·01
Tullbergia krausbaueri-moisture	−0·2205	—	−0·2186	—	−0·2742	—	−0·2638	—
Tullbergia krausbaueri-ignition loss	−0·0037	—	0·1684	—	−0·1041	—	0·1032	—
4 spp.-moisture	0·4145	0·1	0·1966	—	0·4093	—	0·2304	—
4 spp.-ignition loss	−0·2430	—	0·0155	—	−0·3425	—	0·2238	—

In certain cases in this table the values for 20 September 1937 and the drys, though not separately significant, can be combined to give a significant value. In some cases where all four values, both wet and dry, are insignificant but much the same, they can be combined to give a significant value.

Table 4. *Combined partial correlations—horizontal distribution*

	Drys		All values	
		P		*P*
Onychiurus ambulans-ignition loss	−0·3426	0·05–0·02	—	—
Tullbergia krausbaueri-moisture	—	—	−0·2468	0·05
4 spp.-moisture	—	—	0·3055	0·01

From these tables the following facts emerge. The numbers of *O. armatus* are positively correlated with moisture in the wet season, but are indifferent in the dry. From this it need not be inferred that *O. armatus* has some unusual hydrophilic response to very wet soil. It is more likely that it is attracted by some other soil factor which happens to be associated with the wet patches. It is worth recalling that Fidler (1936) found that with chafer larvae there is a steady rise in the tolerated temperature as the soil water increases up to 60% saturation, though above this point there is a rapid decrease. Some similar relationship might easily account for the at first sight peculiar response of *O. armatus*. On the other hand, *O. armatus* is not to be regarded as drought-hardy from its indifference to moisture in the dry season. The soil moisture at no time fell below 29%, and it is probable (Keen, 1931, p. 290) that the moisture content of such a soil would have to fall well below 10% before the soil atmosphere ceased to be saturated.

The numbers of *O. ambulans* are correlated with soil moisture in the dry season, but cannot be shown to be so in the wet. In the dry season they are negatively correlated with ignition loss. *T. krausbaueri* appears to be unaffected by the seasons and to avoid moist places at all times. The four species considered together, on the other hand, show a positive correlation with moisture when all values are combined. The position of *T. quadrispina* is anomalous. Whereas in the three other species the "wets" value has agreed with that for

11 November 1936, and the "drys" value with that for 20 September 1937, in *T. quadrispina* this is not so. The correlations with both moisture and ignition loss differ in sign in each case, and the differences between 20 September 1937 and the "drys" are very significant, though the differences between 11 November 1936 and the "wets" are not significant. This discrepancy is quite extraordinary and no explanation can be offered.

From these correlations we see that no two of the four species have the same reactions to moisture and ignition loss, and that the reactions of the four species considered together are not a guide to the reactions of any one species. The correlations do not at all explain the aggregations present on 11 November 1936, for at that time both moisture and ignition loss appeared to be randomly distributed. But on 20 September 1937 moisture and ignition loss were correlated and in patches. *O. armatus* was indifferent to both of them and was distributed at random. *O. ambulans* was positively correlated with moisture, negatively but less strongly with ignition loss, and apparently the effect of moisture dominates and it is strongly aggregated. *T. quadrispina* behaves anomalously. *T. krausbaueri* is negatively correlated with moisture and so presumably gathers in dry places.

Thus the wet weather aggregations are not explained by reactions of the animals to moisture or ignition loss. The dry weather aggregations may be partly so explained, though it is probable that even here the explanation is far from complete. It is unfortunate that the two samples were taken such a long time apart, for there is no evidence that *O. armatus* was not in aggregations over a foot in diameter on 11 November 1936, or that it was in small aggregations on 20 September 1937. All that we can say is that *O. armatus* was in aggregations of the order of 3 in. diameter on 11 November 1936, and that on 20 September 1937 it was not in aggregations of the order of 12 in. diameter.

An investigation of the effects of liming the soil, on some sample plots, showed that on the whole liming had little influence on numbers. On application of the z and t tests, it was found that only in the case of *T. krausbaueri* was the effect of liming significant (P 0·02–0·01). For the other three species and for the four species together, there was not a significant difference between the limed and the unlimed plots.

6. Choice of sample size

In any investigation involving sampling a large population, there is always a conflict between the ideal of a high degree of accuracy and the labour involved in attaining that ideal. This conflict can best be resolved by studying the most efficient way of using a given amount of labour, and the increase of accuracy to be gained at any time by increasing the labour. Thus, if only a certain time is available for taking one sample, the sampling should be so planned as to give the most accurate possible estimate of the population, and at the same time the most accurate possible statistical estimate of the accuracy attained. On the other hand, if the time for sampling is not strictly limited, it should be ascertained whether or not an increase in size of sample will be accompanied by a proportionate increase in accuracy. For example Jones (1937) was able to show that, in sampling certain wireworm populations, very little additional accuracy was obtained by taking a sample of 100 units, instead of one of 50 units, although 50 units were very much more accurate than 25. In other, denser, populations it was necessary to take only 30 units, for the extra

accuracy obtained by taking more was not commensurate with the additional labour involved.

In the present investigation the three borings taken from any plot on any occasion were mixed and then put through the Ladell's apparatus together. This saved a good deal of labour, and did not affect the real accuracy of the resultant figures for the population. On the other hand it did seriously affect the statistical estimate of the accuracy, and in this way was responsible for considerable loss of information. But when the experiment was planned it was decided to sacrifice this information in order that the samples could be stratified and the vertical distribution studied. As it turned out, the information gained on vertical distribution was probably less interesting than the information lost on horizontal distribution, but there was, of course, no means of knowing this beforehand.

On two occasions, however, separate counts for each boring are available for each of the four species studied. From these data (Tables 1 and 2) the relative standard error has been calculated, by expressing the standard error as a percentage of the mean, the standard error being calculated from the formula

$$\text{S.E.}^2 = \frac{\sigma^2}{N}$$

where σ is the standard deviation, and N the number of units in the sample. As explained, although 18 borings were taken on each of these occasions, they were not 18 independent borings, but 9 random pairs. It is therefore not possible to calculate the standard error with $N = 18$, but only for two parallel series in each of which $N = 9$. In the sample taken on 11 November 1936 (but not in that of 20 September 1937) the two members of a pair of borings were touching. It is therefore possible to regard them together as a single sample of area 16 sq. in. (103 sq. cm.). Moreover, by substituting other values of N in the formula, it is possible to estimate the accuracy obtainable by increasing the number of units in the sample. Table 5 gives the relative standard errors, calculated from the data in Tables 1 and 2, of the west members of the pairs, the east members of the pairs, and in the case of the sample on 11 November 1936, the pair totals. Besides the actual standard error is given the estimate of what the standard error would be if the number of borings were increased to 16 or 25. The standard error is an expression of the accuracy of the mean of a sample. It implies that the true population lies within the limits of the mean plus or minus twice the standard error.

These high relative standard errors proceed directly from the very irregular distribution which has already been discussed. It is noticeable that increasing the number of units in the sample would greatly increase the accuracy of the estimate of the population of each of the four species, but when they are considered together as Onychiuridae, 25 borings would be little better than 16, and 16 not a great deal better than 9. It is also noticeable that doubling the

size of the sampling unit (as in the row "W.E. total") has very little effect on the accuracy: it is possible that a smaller unit would be nearly as accurate. But *Onychiurus ambulans* is so irregularly distributed that although on 20 September 1937 it had the highest mean population of any Onychiuridae, it was entirely absent from one of the borings. If the size of the sampling unit were decreased too much the number of zero counts might increase rapidly, and this would lower the accuracy considerably.

Table 5. *Relative standard errors, from data of Tables* 1 *and* 2

Date	Series	N	*Onychiurus armatus*	*Onychiurus ambulans*	*Tullbergia quadrispina*	*Tullbergia krausbaueri*	Onychiuridae
11 Nov. 1936	W.	9	21·89	23·02	15·53	29·54	11·19
		16	16·42	17·27	11·64	22·16	8·39
		25	13·13	13·81	9·32	17·73	6·71
	E.	9	34·61	18·18	25·03	28·97	10·18
		16	25·95	13·63	18·73	22·65	7·64
		25	20·76	10·91	14·99	18·11	6·11
	W.E.	9	27·52	19·64	18·73	29·02	7·90
	total	16	20·64	14·73	13·75	21·76	5·91
		25	16·51	11·78	11·00	17·41	4·74
20 Sept. 1937	W.	9	11·03	22·73	18·43	25·00	10·10
		16	8·28	17·05	13·82	18·76	7·58
		25	6·62	13·64	11·30	14·50	6·06
	E.	9	20·89	30·04	37·80	11·74	10·85
		16	15·66	22·53	28·35	8·78	12·63
		25	12·53	18·03	22·68	7·02	10·11

It is not possible to generalize on the subject of the ideal size of a soil sample. The best size and composition of a sample to take will be dependent upon the population to be studied, the character of the soil, and in particular upon the information which is being sought.

7. Vertical distribution

In Table 6, the figures for the upper two layers are the means of 20 samples, those for the third layer the means of 15 samples, weighted to make them correspond with the others. Those for the bottom layer are derived from only three partial samples, equivalent to one whole sample.

Table 6. *Mean vertical distribution of Collembola*

Depth in.	*Onychiurus armatus*	*Onychiurus ambulans*	*Tullbergia quadrispina*	*Tullbergia krausbaueri*	"Other Collembola"	All Collembola
0–4·5	151	181	66	101	320	819
4·5–9	73	185	82	54	67	461
9–13·5	30	117	68	25	28	268
13·5–16	2	36	36	11	2	67

Fig. 1 shows these distributions graphically. It emphasizes the distinction already insisted upon, between Onychiuridae as subterranean animals and other Collembola as surface dwellers. Actually it is probably not quite an accurate picture of the distribution of "other Collembola". The lower layers

were sampled by putting the borer back in the hole left after taking the upper sample. The hole was thus left open for a few minutes, during which time nothing was done to prevent Collembola from the surrounding vegetation from jumping into it. When the lower layer was removed such Collembola would, of course, be recorded as belonging to that layer. Thus the circumstance that the technique was not specially planned to deal with "other Collembola" has produced in these animals the appearance of a deeper distribution than they really have.

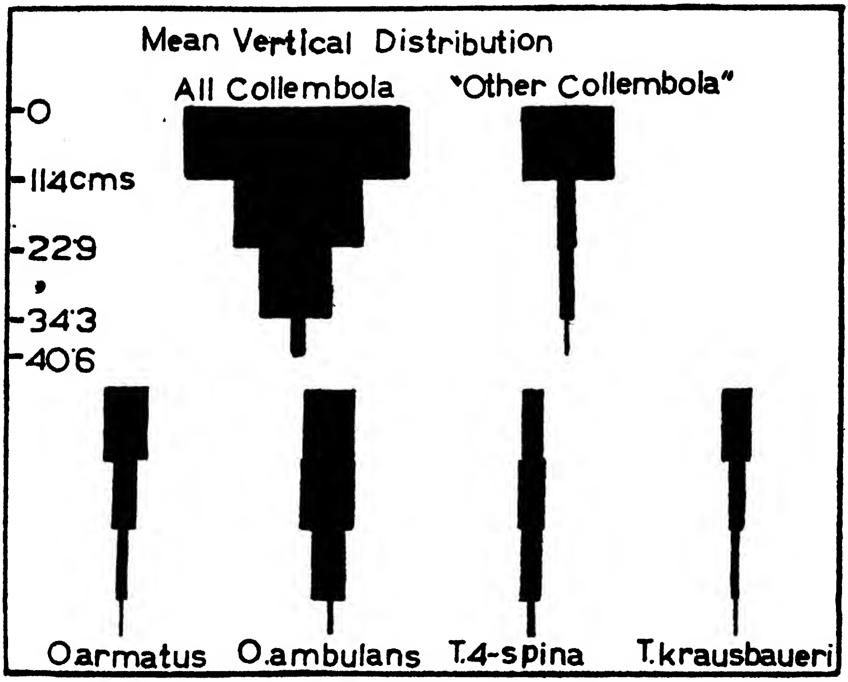


Fig. 1.

Fig. 1 emphasizes once more the differences which exist between closely related species. *Tullbergia quadrispina* is almost equally abundant in the first three layers. Frenzel (1936) also found that it had a remarkably deep distribution, and that at a depth of 15–25 cm. it was the sole representative of the order.

Onychiurus ambulans makes considerable migrations, and is only rarely in the mean condition of Fig. 1. The other three species always kept approximately to the distribution shown. Fig. 2 shows the seasonal migrations of *O. ambulans*. With it are plotted the saturation deficiency of the soil in three $4\frac{1}{2}$-in. layers, and the soil temperatures at 10 cm. and 75 cm. depth. The saturation deficiency is a measure of the dryness of the soil. The value is obtained by subtracting the moisture content at the time from the moisture content when the soil is saturated. Since the saturation point of the upper

soil is much higher than that of the lower, equal values for the moisture content correspond to a much higher saturation deficiency in the upper layer.

The seasonal migrations of *O. ambulans* are not extensive, that is to say, at no time does it completely vacate a layer in which it is abundant at another time, but it does have a distinct tendency to live at greater depths in summer and winter than it does in spring and autumn. It is not very easy to relate this movement to physical changes. It seems reasonable to suppose that the downward trend in summer is in search of greater moisture, for in considering

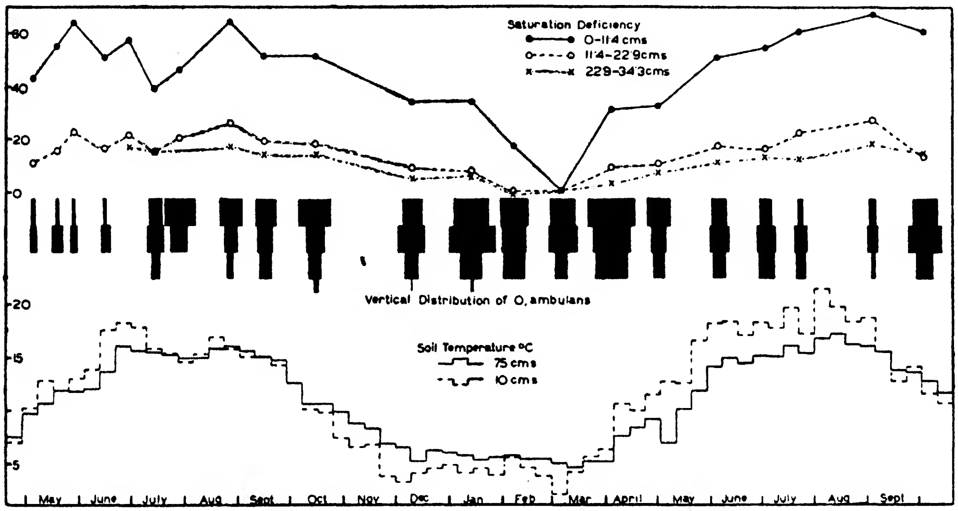


Fig. 2.

the horizontal distribution a correlation was found between this species and moisture in dry conditions. But the two cases are not necessarily comparable. When one layer of soil is damper than another it is a simple reversible difference with no further implications; but when one patch of soil is damper than another a few feet away it is likely to be associated with other differences. We know it is in fact associated with differences in ignition loss, and have eliminated the effect of this factor, but we do not know whether it is associated as well with some other factor such as pore-space. However, in the absence of any other information it seems reasonable to suggest that the summer descent may be a response to surface dryness.

It seems unlikely that moisture is important in the winter descent. It is noticeable that all the time the animals are in the winter deep position the deep temperature exceeds the shallow temperature. On the other hand no correlation was found (see below) between temperature and the populations of *O. ambulans*. Still, it is quite possible that *O. ambulans* does become sensitive to temperature when the temperature is low, for if such a relation did exist it would occur in too few of the samples to be apparent in the general correlation. So it is suggested that when, in winter, the surface of the ground becomes cold, *O. ambulans* tends to descend to where it is warmer.

Frenzel (1936) could not detect vertical movements in any of the groups of animals in his meadow. Bryson (1935) found that wireworms in Kansas moved down in summer and in winter, just as *O. ambulans* does, and ascribed the movement to temperature in each case. McColloch & Hayes (1923) found that white grubs and May beetles moved down in winter and up in summer, so that they were always in the warmer layer.

8. Population fluctuations

Samples were taken during the 19 months from April 1936 to October 1937. The results of these samples are given in Figs. 3 and 4. All the curves refer to the population to a depth of 9 in. (23 cm.) as the early samples were taken no deeper than this. Inclusion of the 9–13½ in. layer would not have affected the general character of the curves, except to increase the relative heights of the peaks of *O. ambulans*.

From the data were calculated correlation coefficients between the populations and the soil temperature and the soil moisture. As the soil moisture is strongly correlated with temperature, it was important to eliminate the effect of each of these variables when considering the other. Table 7 gives the partial correlations of the populations, with temperature with the effect of moisture eliminated, and with moisture with the effect of temperature eliminated. The temperature is the soil temperature at 25 cm., the value being the mean of the readings for the 100 days before the sample was taken.

Table 7. *Partial correlations of populations with soil moisture and temperature (100 day mean). The value of* P *is given where it is* 0·05 *or less*

	Moisture	*P*	Temperature	*P*
Onychiurus armatus	0·5783	0·01	0·5825	0·01
Onychiurus ambulans	0·4782	0·05–0·02	0·3113	—
Tullbergia quadrispina	0·2193	—	−0·0093	—
Tullbergia krausbaueri	0·4707	0·05	0·4603	0·05–0·02
Onychiuridae	0·6317	0·01	0·5301	0·01
Three species*	0·5516	0·01	0·5351	0·01
"Other Collembola"	−0·0431	—	0·6022	0·01
Moisture-temperature (total correlation)	−0·6319	0·01	—	—

* A total of *O. armatus*, *T. quadrispina*, *T. krausbaueri*.

Correlations were also calculated between the populations and the temperature means for 56, 28 and 14 days before sampling. The values obtained have, of course, different values for the partial correlation with moisture, and generally speaking neither were significant. Table 8 gives the few partial correlations which were significant, based on the mean temperature of 56 or 28 days. None of the partial correlations based on the mean temperature of the previous 14 days were significant.

The temperature correlations increased, the greater the mean number of days for which they were calculated. The partial correlation coefficients of

Table 8. *Partial correlations of populations with soil moisture and temperature (means of 56 and 28 days)*

	Moisture	P	Temperature	P
	(*a*) Mean temperature of previous 56 days			
Onychiurus armatus	0·5676	0·01	0·5437	0·01
Three species*	0·4484	0·05–0·02	—	—
	(*b*) Mean temperature of previous 28 days			
Onychiurus armatus	0·4745	0·05–0·02	0·4200	0·05
Three species*	0·4474	0·05–0·02	—	—

* Total of *O. armatus*, *T. quadrispina*, *T. krausbaueri*.

T. krausbaueri, a typical case, for the temperature means of the previous 14, 28, 56 and 100 days were respectively 0·0718, 0·1781, 0·3324, 0·4603. Thus, with certain exceptions, there is a significant partial correlation between each species and moisture and temperature. The exceptions are *O. ambulans*, which is not significantly correlated with temperature, the group "other Collembola" which is not significantly correlated with moisture, and *T. quadrispina*, which is not significantly correlated with either. It is worth recalling at this point the limitations of the statistical method. Absence of proof of a proposition does not imply proof of the converse. The partial correlations *O. ambulans*-temperature (0·3113) and *T. quadrispina*-moisture (0·2193) are not significant, but at the same time they are not significantly different from the corresponding correlations of *O. armatus*. That is to say the evidence available is not sufficient to enable one to say that the populations of *O. ambulans* and *T. quadrispina* are correlated differently from that of *O. armatus*, and it is quite possible that a more thorough investigation comprising a greater number of samples would reveal a significant correlation both for *O. ambulans*-temperature and *T. quadrispina*-moisture. On the other hand the partial correlations *T. quadrispina*-temperature and "other Collembola"-moisture are significantly different from the corresponding correlations of *O. armatus*. Though one cannot affirm that these populations are indifferent to temperature and moisture respectively, one can say that their relation to these factors is different to that of *O. armatus*, which can be specified. Further investigation might reveal a positive correlation, though this would have to be very small to fulfil the condition of difference from *O. armatus*, or a negative correlation; but since the observed correlations are so nearly zero, there is a presumption (but only a presumption) that within the limits of the observations *T. quadrispina* is indifferent to temperature, and "other Collembola" to moisture.

The partial correlations of Table 7 above are not, however, of great assistance in interpreting the population fluctuations shown in Figs. 3 and 4. This is on account of the large negative correlation between temperature and moisture. In practice these two factors almost entirely cancel one another out.

Table 9 shows the result of calculating the total correlation of the populations with moisture and temperature without eliminating the effect of these

variables upon each other. We see that in the majority of cases these two factors have interfered with each other to such an extent that we can no longer regard their influence as being significant. A period of high temperature, which favours the animals, coincides with drought which inhibits them, and vice versa. Exceptions to this are the Onychiuridae, and the "other Collembola". The Onychiuridae show a positive total correlation with moisture, and Fig. 3 demonstrates how they are at a maximum in the wet season and fewer in the dry (see Fig. 2). Actually the minimum of Onychiuridae, as of all other groups, was in April 1936, which was not a dry period. This phenomenon will be discussed later.

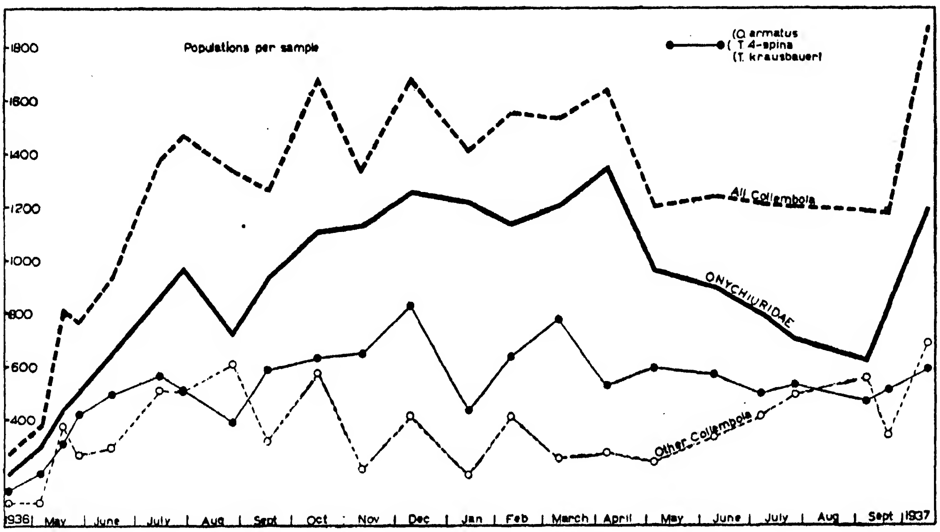


Fig. 3.

Table 9. *Total correlations of populations with temperature (100 day mean) and soil moisture*

	Moisture	*P*	Temperature	*P*
Onychiurus armatus	0·2594	—	0·2721	—
Onychiurus ambulans	0·3824	—	−0·0187	—
Tullbergia quadrispina	0·2852	—	−0·1872	—
Tullbergia krausbaueri	0·1541	—	0·2551	—
Onychiuridae	0·4175	0·05	0·1095	—
Three species*	0·2736	—	0·2261	—
"Other Collembola"	−0·4720	0·05–0·02	0·7097	0·01

* Total of *O. armatus*, *T. quadrispina*, *T. krausbaueri*.

"Other Collembola" are positively correlated with temperature and negatively with moisture, so they should be most numerous in summer. Their curve on Fig. 3, in spite of violent fluctuations, tends to an autumn peak and a spring minimum. Since the temperature relation is a long-term effect, the violent fluctuations which are so noticeable from August to February cannot be due to this cause. The effect of moisture (Table 9) is apparent, not real (Table 7) so that this factor is not responsible either. Analysis of the population

fluctuations of Onychiuridae makes one disinclined to press any further enquiry into the causes of fluctuations in the wide and indefinite group "other Collembola".

Fig. 4 shows that the four species of Onychiuridae, which have already been shown to be so different with respect to horizontal and vertical distribution, are also extremely different with respect to population fluctuations. The most striking case is that of *Onychiurus ambulans*, whose peak population is thirteen times the minimum, while the peak of the Onychiuridae as a whole is only seven times the minimum. It was shown in Table 7 that *O. ambulans* was correlated with moisture, but not that it was correlated with temperature. The assumption that moisture was more important to it than temperature

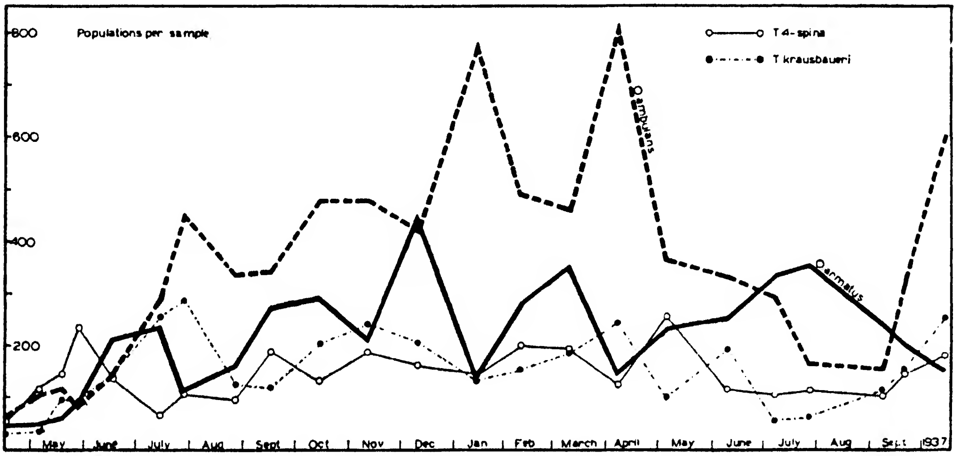


Fig. 4.

Table 10. *Soil temperature at 25 cm.: means of preceding periods*

	14 days	28 days	56 days	100 days
20 Apr. 1936	5·13	6·29	5·13	3·93
5 May 1936	7·56	6·37	6·32	4·67
18 May 1936	10·88	9·12	7·78	5·64
28 May 1936	12·11	11·00	8·48	6·76
16 June 1936	12·54	12·11	10·78	8·62
14 July 1936	16·36	16·48	14·29	11·46
28 July 1936	15·23	15·79	15·18	12·88
27 Aug. 1936	15·84	15·48	15·60	14·77
16 Sept. 1936	15·04	15·51	15·34	15·52
15 Oct. 1936	8·23	11·01	13·20	14·19
11 Nov. 1936	7·44	8·34	9·78	12·28
10 Dec. 1936	4·60	5·49	6·88	9·34
13 Jan. 1937	4·82	4·94	4·79	6·17
10 Feb. 1937	4·36	4·54	4·74	5·08
10 Mar. 1937	2·94	3·71	4·13	4·34
7 Apr. 1937	4·46	4·03	3·88	4·19
5 May 1937	9·23	8·75	6·35	5·32
9 June 1937	14·57	12·66	10·88	7·84
7 July 1937	15·43	15·28	13·97	11·23
27 July 1937	16·22	15·74	15·40	13·18
7 Sept. 1937	16·20	16·80	16·65	15·99
20 Sept. 1937	14·10	15·18	16·10	15·86
16 Oct. 1937	11·05	11·69	13·51	14·88

would account for the high winter populations of this animal, which at other seasons was not more numerous than other Onychiuridae.

The peak of *Onychiurus armatus* is ten times the minimum. As with *O. ambulans* its maximum occurs in winter. Both in 1936 and 1937 it had another peak in July. This species has a high partial correlation with both temperature and moisture, and taken over the whole period these two factors nullify one another (Table 9). But lacking knowledge of the moisture reactions at low temperatures or the temperature reactions at low moistures, we cannot deny that these factors may be responsible for the winter and summer peaks respectively.

Tullbergia quadrispina at its peak is only five times its minimum. It has a peak in May followed by a depression in July, August and September of both years. From October to April the population is steady. This is the only species showing no significant correlation with either moisture or temperature, and this is reflected in the fact that it is in numbers the least variable species. *Tullbergia krausbaueri* has a peak ten times its minimum. The peaks occur about every four months, in July, November, April, June and October. This species has a significant partial correlation with both moisture and temperature, but taken over the whole period these two factors cancel each other out, and as with *O. armatus*, it is impossible to say whether a more detailed knowledge of the temperature-moisture reactions would do much to explain these population fluctuations, or whether other factors are mainly responsible. The three species *O. armatus*, *T. quadrispina* and *T. krausbaueri* agree in having a low January population, and their populations are in general not dissimilar during the winter months. The curve of the total of these three species (Fig. 3) has a pronounced double winter peak, with an intervening minimum in January. By the t test the January population is significantly less than the mean of the December, February and March populations (P 0·05–0·02). The double peak in this curve can therefore be regarded as significant, unlike the conspicuous double peaks in the curves of *O. armatus* and *O. ambulans*. In neither of these cases are the minima significantly less than the surrounding peaks.

Review of the literature led Ford (1937*a*) to the tentative conclusion that such a double winter fluctuation as we have here in the combined population of *O. armatus*, *T. quadrispina* and *T. krausbaueri* is a general characteristic of populations of Collembola. The data present here are favourable to Ford's hypothesis, but do not offer it any strong support. The significant dip in the "three species" curve cannot be regarded as very important, for we have no good grounds for grouping these three species together. As already noted, the dips in the curves of *O. armatus* and *O. ambulans* cannot be regarded as significant.

In February and March, as shown in Fig. 2, the ground was extremely wet, and in March became completely waterlogged. The holes left after

sampling filled up with water, pools of water lay about on the plots. The Onychiuridae were apparently unaffected by this flooding. Ordinarily it is impossible to wet the animals with water: it is possible that they carried an air-bubble round them throughout the flooded period. In February 5·34 in. of rain fell, in March 3·08. This rain, which was well distributed, would probably keep the soil water fairly well aerated. Ingram (1931) by flooding was able to exterminate soil animals, including *Onychiurus armatus*, in sugar-cane fields, but doubtless high temperatures obtain in Louisiana.

As samples were taken during only 19 months, it is not possible to say much about annual, as opposed to seasonal, population fluctuations. But it is remarkable that the only feature which all the Onychiuridae have in common, and in which they agree with "other Collembola" is that their minimum was in April 1936. The winter of 1935–6 was colder than that of 1936–7 and the surface of the ground was for some time frozen solid to a depth of several inches. Probably this cold reduced the whole Collembolan population.

It has been the custom to express soil populations in millions per acre. When at their peak the Onychiuridae reached a density of 117 millions per acre. This statement gives a false impression of enormous abundance. It actually implies a density of one animal to 8 c.c. of soil, of which 20–40% can be regarded as habitable pore-space. The custom of expressing population densities with reference to area can be extremely misleading, and greater care should be taken to refer them to the real environment. Thus Baweja, in his study of recolonization after soil sterilization, refers (his Table 12) populations to area, and records for Collembola an increase of 1·6–2·2 over the control. Yet elsewhere (p. 92) he records that Onychiuridae failed to regain their normal strength. The Onychiuridae are soil dwellers and two populations may perhaps be legitimately compared on an area basis. But the other Collembola, such as Hypogastruridae, Entomobryidae and Isotomidae, live in the bottom of the vegetation. Their population density must be calculated on a basis which makes allowance for the density of that vegetation. Baweja's photographs show that there was a very much stronger growth of vegetation on his sterilized plots than on the controls, owing to the effect of heat sterilization on the soil. In other words there was more vegetation for the Collembola to live on. Had he made allowance for this by calculating the population density on some such basis as the weight of vegetation per sample, it is quite possible he would have found no difference in density between experiment and control.

The highest density of population per unit volume is summarized in Table 11. None of these are very high populations in the absolute sense. Park (1938) for instance, found 32 g. of flour supporting 89 live *Tribolium confusum*, or nearly 3 per gram, an incomparably denser population, in terms of biomass, than anything present in the soil. The figures in columns A, α–γ, represent the density in the areas of maximum population density. As they are derived from the totals of three independent borings, higher densities

than those shown no doubt actually occur. These figures may probably be halved to give a fair estimate of the number of c.c. supporting one animal, in the closest aggregations found.

Table 11. *Number of cubic centimetres of soil containing one animal*

A, maximum recorded density from any plot at any time.
B, peak population, mean of largest sample.
C, mean population.
D, minimum population.

α, 0–11·4 cm.
β, 11·4–22·9 cm.
γ, 22·9–34·3 cm.

	A			B			C			D		
	α	β	γ	α	β	γ	α	β	γ	α	β	γ
Onychiurus armatus	7	20	35	15	61	204	35	73	177	183	253	—
Onychiurus ambulans	6	7	12	12	15	18	29	29	45	379	74	—
Tullbergia quadrispina	23	18	19	36	47	50	80	65	78	279	113	190
Tullbergia krausbaueri	20	24	61	27	59	—	53	98	212	83	156	—
Onychiuridae	4	6	8	7	9	13	11	13	22	36	35	—

9. Summary

1. Samples were taken from a coarse long-neglected meadow at Slough at intervals over 19 months. The fauna was separated by means of a large Ladell apparatus. In the truly subterranean fauna the most important group was the Onychiuridae, of which there were four species, *Onychiurus armatus*, *Onychiurus ambulans*, *Tullbergia quadrispina* and *Tullbergia krausbaueri*.

2. None of the four species is distributed at random in the soil. All are aggregated, the size of the colonies being for *O. armatus* about 3 in. diameter, for the other species at least 12 in. diameter. Under wet conditions the distribution of *O. armatus* is positively correlated with soil moisture, and under dry conditions *O. ambulans* is positively correlated with moisture, and negatively with the ignition loss of the soil. The correlations do not fully account for the uneven distribution of the animals.

3. It is shown that owing to the uneven distribution of the animals, it is necessary to take a sample composed of a large number of small units, in order to get an accurate estimate of the population.

4. The vertical distribution of each of the species is different. *O. ambulans* and *T. krausbaueri* are most numerous near the surface, their numbers falling off gradually. *T. quadrispina* is evenly distributed to a depth of 13½ in. (34·3 cm.) below which depth it is more rare. *O. ambulans* shows seasonal changes in vertical distribution, in spring and autumn it is most plentiful near the surface, while in summer and winter it is more abundant deeper down. It is suggested that the summer alteration is occasioned by dryness, the winter by temperature.

5. The populations of each species show positive partial correlations with soil moisture and temperature, except in the case of *O. ambulans*, which is independent of temperature, and *T. quadrispina*, which is not significantly correlated with either moisture or temperature. As these factors are themselves negatively correlated, however, their effects cancel each other out, and

population fluctuations cannot with certainty be attributed to either. The populations of both species of *Onychiurus* show winter maxima. The effect of freezing and flooding on the populations is also discussed.

6. The most appropriate standard of reference of the population density is discussed, and the population is expressed in terms of volume of soil, though it is recognized that it would be better expressed in terms of pore-space. The peak density of Onychiuridae corresponded to one animal to 8 c.c. of soil.

7. In every case the species were found to have widely differing properties, and the reactions of one species, or of the group Onychiuridae, were no guide to the reactions of the other species.

8. In Appendix 2 a convenient type of soil sampler is described; there is also a discussion of the advantages of the Ladell apparatus on p. 327.

APPENDIX 1. CENSUS COUNTS

Samples taken in the Pond Field at the Biological Field Station, Slough, between April 1936 and October 1937

α, 0–4·5 in. (0–11·4 cm.). γ, 9–13·5 in. (22·9–34·3 cm.).
β, 4·5–9 in. (11·4–22·9 cm.). δ, 13·5–16 in. (34·3–40·6 cm.).

Onychiurus armatus

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	14	10	—	—	13	7	—	—	2	4	—	—
18 May 1936	6	9	—	—	19	7	—	—	6	15	—	—
28 May 1936	9	15	—	—	11	13	—	—	23	20	—	—
16 June 1936	9	21	—	—	38	24	—	—	63	57	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	30	16	8	—	45	25	9	—	72	51	24	—
28 July 1936	44	6	—	—	22	16	—	—	11	16	—	—
27 Aug. 1936	33	25	9	—	18	19	7	—	31	36	2	—
16 Sept. 1936	30	20	11	—	48	17	10	—	74	87	24	—
15 Oct. 1936	48	29	21	—	95	47	3	—	47	27	10	2
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	40	27	10	—	72	14	8	0	250	46	8	—
13 Jan. 1937	35	7	5	1	37	2	0	—	51	14	3	—
10 Feb. 1937	52	13	5	—	60	4	1	—	111	40	6	—
10 Mar. 1937	99	21	5	—	21	2	1	—	183	25	18	—
7 Apr. 1937	78	20	8	—	6	3	1	—	35	8	0	—
5 May 1937	35	8	14	—	33	3	2	—	108	46	23	—
9 June 1937	53	14	19	—	46	8	6	—	88	42	34	—
7 July 1937	108	73	43	—	27	12	6	—	72	41	23	—
27 July 1937	18	29	51	—	69	50	15	—	118	72	12	—
7 Sept. 1937	51	34	14	—	55	40	13	—	41	25	10	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	20	15	6	—	60	16	8	—	25	16	8	—

Onychiurus ambulans

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	24	41	—	—	4	8	—	—	15	11	—	—
18 May 1936	13	28	—	—	11	12	—	—	4	59	—	—
28 May 1936	5	34	—	—	5	18	—	—	4	20	—	—
16 June 1936	13	56	—	—	23	32	—	—	15	6	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	63	50	31	—	4	23	11	—	64	89	41	—
28 July 1936	222	17	—	—	19	48	—	—	56	91	—	—
27 Aug. 1936	99	62	34	—	52	40	16	—	49	37	13	—
16 Sept. 1936	148	93	78	—	30	26	19	—	21	26	31	—
15 Oct. 1936	131	62	46	—	32	28	9	—	142	84	63	17
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	103	152	75	—	28	24	15	1	53	65	28	—
13 Jan. 1937	226	268	118	5	15	13	6	—	95	165	97	—
10 Feb. 1937	198	113	119	—	20	55	55	—	47	62	54	—
10 Mar. 1937	156	124	65	—	32	24	12	—	49	78	30	—
7 Apr. 1937	157	126	137	—	22	32	14	—	273	207	149	—
5 May 1937	188	132	97	—	31	12	2	—	2	1	2	—
9 June 1937	74	101	56	—	32	30	18	—	41	54	52	—
7 July 1937	97	145	137	—	11	27	17	—	14	11	10	—
27 July 1937	9	40	60	—	11	21	16	—	23	63	15	—
7 Sept. 1937	30	38	26	—	14	33	7	—	18	29	7	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	169	213	104	—	71	43	43	—	48	59	16	—

Tullbergia quadrispina

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	36	35	—	—	11	22	—	—	5	5	—	—
18 May 1936	15	19	—	—	38	45	—	—	10	21	—	—
28 May 1936	36	101	—	—	22	52	—	—	13	11	—	—
16 June 1936	9	26	—	—	33	39	—	—	25	7	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	2	15	6	—	1	13	13	—	16	19	22	—
28 July 1936	35	7	—	—	11	27	—	—	5	21	—	—
27 Aug. 1936	15	21	9	—	11	20	10	—	9	22	3	—
16 Sept. 1936	43	53	62	—	38	28	22	—	10	18	10	—
15 Oct. 1936	21	20	36	—	22	14	12	—	24	31	24	10
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	32	24	18	—	36	23	93	28	32	16	5	—
13 Jan. 1937	13	11	8	0	44	21	19	—	33	26	18	—
10 Feb. 1937	15	21	33	—	44	81	77	—	24	17	12	—
10 Mar. 1937	51	54	49	—	20	29	30	—	17	27	27	—
7 Apr. 1937	22	23	15	—	16	20	15	—	17	29	29	—
5 May 1937	59	72	81	—	77	29	21	—	11	11	4	—
9 June 1937	9	12	5	—	22	47	6	—	19	30	14	—
7 July 1937	18	16	27	—	6	31	14	—	10	25	14	—
27 July 1937	3	7	10	—	17	65	30	—	6	15	1	—
7 Sept. 1937	4	6	4	—	15	45	13	—	19	14	17	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	16	19	30	—	67	50	54	—	16	13	15	—

Tullbergia krausbaueri

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	8	6	—	—	8	1	—	—	6	1	—	—
18 May 1936	24	1	—	—	24	12	—	—	16	21	—	—
28 May 1936	8	4	—	—	17	21	—	—	24	18	—	—
16 June 1936	8	15	—	—	23	47	—	—	29	23	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	34	26	6	—	88	52	13	—	42	15	9	—
28 July 1936	80	2	—	—	54	15	—	—	65	73	—	—
27 Aug. 1936	22	13	9	—	32	15	8	—	37	8	3	—
16 Sept. 1936	39	22	6	—	23	14	14	—	13	9	13	—
15 Oct. 1936	12	6	4	—	56	24	10	—	74	33	12	5
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	3	17	8	—	76	23	29	7	65	25	29	—
13 Jan. 1937	22	13	9	2	45	6	0	—	19	29	22	—
10 Feb. 1937	38	9	17	—	55	16	26	—	18	18	0	—
10 Mar. 1937	45	12	9	—	44	13	1	—	20	10	3	—
7 Apr. 1937	15	27	11	—	28	18	7	—	87	72	36	—
5 May 1937	27	15	4	—	29	3	6	—	20	7	0	—
9 June 1937	44	10	2	—	18	18	0	—	78	43	13	—
7 July 1937	13	5	2	—	24	5	2	—	8	4	1	—
27 July 1937	6	2	7	—	23	10	4	—	15	8	0	—
7 Sept. 1937	29	4	2	—	28	13	3	—	27	5	3	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	30	18	6	—	86	31	12	—	65	30	11	—

Onychiuridae (four species)

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	82	92	—	—	36	38	—	—	30	21	—	—
18 May 1936	60	57	—	—	93	76	—	—	36	116	—	—
28 May 1936	58	154	—	—	55	104	—	—	64	69	—	—
16 June 1936	39	118	—	—	117	142	—	—	132	93	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	129	107	51	—	138	113	46	—	194	174	96	—
28 July 1936	381	32	—	—	106	106	—	—	137	201	—	—
27 Aug. 1936	169	121	71	—	113	94	41	—	126	103	21	—
16 Sept. 1936	260	188	157	—	139	85	65	—	118	140	78	—
15 Oct. 1936	212	117	107	—	205	113	34	—	287	175	109	34
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	178	220	111	—	212	84	145	38	400	152	70	—
13 Jan. 1937	296	299	140	10	141	42	25	—	198	234	134	—
10 Feb. 1937	303	156	174	—	179	156	159	—	200	137	72	—
10 Mar. 1937	351	211	128	—	117	68	44	—	269	140	78	—
7 Apr. 1937	272	196	171	—	72	73	37	—	412	316	214	—
5 May 1937	309	227	196	—	170	47	31	—	141	65	29	—
9 June 1937	180	139	82	—	118	63	30	—	226	169	113	—
7 July 1937	236	239	209	—	68	75	39	—	94	81	48	—
27 July 1937	36	78	128	—	120	146	65	—	162	158	28	—
7 Sept. 1937	114	82	46	—	112	131	36	—	105	80	37	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	235	265	146	—	278	140	117	—	154	118	50	—

Moisture %

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	56·14	44·72	—	—	57·26	49·08	—	—	42·47	49·82	—	—
18 May 1936	42·98	42·22	—	—	37·89	39·17	—	—	43·87	46·95	—	—
28 May 1936	33·40	38·12	—	—	32·65	35·31	—	—	35·81	37·85	—	—
16 June 1936	48·40	41·39	—	—	46·12	41·40	—	—	43·00	43·52	—	—
30 June 1936	39·60	35·99	38·47	—	34·54	35·25	42·56	—	42·91	40·75	41·34	—
14 July 1936	62·52	42·65	28·70	—	51·30	37·44	39·45	—	56·06	49·27	46·51	—
23 July 1936	56·23	39·33	—	—	49·18	35·28	—	—	43·92	38·92	—	—
27 Aug. 1936	34·08	32·18	33·51	—	29·68	36·90	43·61	—	32·84	27·08	46·05	—
16 Sept. 1936	51·92	38·75	40·09	—	40·79	35·44	44·59	—	41·25	42·41	48·09	—
15 Oct. 1936	50·37	43·77	41·89	—	38·09	37·84	40·21	—	46·58	38·78	48·73	44·75
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	67·54	52·30	51·24	—	55·82	43·05	50·30	48·53	63·08	51·62	56·49	—
13 Jan. 1937	67·98	47·56	54·24	52·36	53·67	39·72	50·47	—	65·66	53·55	52·71	—
10 Feb. 1937	71·09	56·15	66·37	—	72·85	54·28	58·01	—	71·69	62·22	64·77	—
10 Mar. 1937	82·41	59·57	58·20	—	68·10	53·65	55·47	—	138·5	61·25	61·56	—
7 Apr. 1937	65·63	52·44	54·61	—	64·15	52·20	55·65	—	64·01	42·64	55·07	—
5 May 1937	70·25	46·23	49·33	—	50·59	40·34	48·35	—	70·52	56·69	54·59	—
9 June 1937	47·53	38·20	46·59	—	42·01	40·84	47·62	—	48·14	43·73	47·65	—
7 July 1937	42·51	39·93	41·72	—	38·02	42·94	46·55	—	44·30	43·18	47·19	—
27 July 1937	34·80	33·67	46·18	—	39·66	30·95	40·82	—	40·20	42·03	50·99	—
7 Sept. 1937	30·51	29·20	38·41	—	26·57	28·94	37·18	—	30·08	33·67	43·18	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	37·43	34·98	42·98	—	29·71	30·31	41·30	—	40·37	38·23	46·98	—

Ignition loss %

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	15·81	11·27	—	—	14·85	11·81	—	—	15·08	11·73	—	—
18 May 1936	14·27	11·13	—	—	12·76	10·17	—	—	14·34	10·86	—	—
28 May 1936	14·32	11·09	—	—	15·09	9·88	—	—	14·10	11·16	—	—
16 June 1936	14·37	10·67	—	—	13·64	10·89	—	—	12·72	10·22	—	—
30 June 1936	13·59	10·93	9·79	—	14·25	10·85	9·86	—	15·21	12·26	9·54	—
14 July 1936	13·46	10·77	10·72	—	14·51	11·31	10·70	—	13·86	10·84	10·25	—
28 July 1936	—	—	—	—	—	—	—	—	—	—	—	—
27 Aug. 1936	13·85	10·64	9·01	—	13·39	10·57	9·88	—	12·54	9·58	10·35	—
16 Sept. 1936	13·31	10·92	9·49	—	14·30	10·36	9·83	—	13·22	11·46	9·39	—
15 Oct. 1936	12·48	10·40	8·86	—	13·20	11·37	10·17	—	14·78	9·98	10·11	8·85
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	—	—	—	—	—	—	—	—	—	—	—	—
13 Jan. 1937	—	—	—	8·298	—	—	—	—	—	—	—	—
10 Feb. 1937	—	—	—	—	—	—	—	—	—	—	—	—
10 Mar. 1937	—	—	—	—	—	—	—	—	—	—	—	—
7 Apr. 1937	13·20	10·86	9·93	—	13·13	10·98	10·05	—	14·33	10·39	11·40	—
5 May 1937	16·59	9·97	8·92	—	14·23	9·20	9·38	—	15·30	11·44	9·88	—
9 June 1937	13·96	10·68	9·51	—	13·93	9·47	9·33	—	14·28	10·99	8·86	—
7 July 1937	13·91	10·89	9·71	—	13·78	10·77	10·21	—	14·02	11·59	9·73	—
27 July 1937	—	—	—	—	—	—	—	—	—	—	—	—
7 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	—	—	—	—	—	—	—	—	—	—	—	—

Onychiurus armatus

Totals for depths and occasions

	α	β	γ	δ	Total to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	46
5 May 1936	29	21	—	—	50
18 May 1936	31	31	—	—	62
28 May 1936	43	48	—	—	91
16 June 1936	110	102	—	—	212
14 July 1936	147	92	41	—	239
28 July 1936	77	38	—	—	115
27 Aug. 1936	82	80	18	—	162
16 Sept. 1936	152	124	45	—	276
15 Oct. 1936	192	103	34	6	295
11 Nov. 1936	—	—	—	—	213
10 Dec. 1936	362	87	26	0	449
13 Jan. 1937	123	23	14	3	146
10 Feb. 1937	223	57	12	—	280
10 Mar. 1937	303	69	24	—	372
7 Apr. 1937	119	31	9	—	150
5 May 1937	176	57	39	—	233
9 June 1937	187	66	59	—	253
7 July 1937	207	126	72	—	333
27 July 1937	205	151	78	—	356
7 Sept. 1937	147	99	37	—	246
20 Sept. 1937	—	—	—	—	203
16 Oct. 1937	105	47	22	—	152

Onychiurus ambulans

Totals for depths and occasions (see Figs. 2, 3 and 4)

	α	β	γ	δ	Total to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	65
5 May 1936	43	60	—	—	103
18 May 1936	28	99	—	—	127
28 May 1936	14	72	—	—	86
16 June 1936	51	94	—	—	145
14 July 1936	131	162	83	—	293
28 July 1936	297	156	—	—	453
27 Aug. 1936	200	139	63	—	339
16 Sept. 1936	199	145	128	—	344
15 Oct. 1936	305	174	118	51	479
11 Nov. 1936	—	—	—	—	481
10 Dec. 1936	184	241	118	3	425
13 Jan. 1937	336	446	209	15	782
10 Feb. 1937	265	230	228	—	495
10 Mar. 1937	237	258	107	—	495
7 Apr. 1937	452	365	300	—	817
5 May 1937	221	145	101	—	366
9 June 1937	147	185	126	—	332
7 July 1937	112	183	164	—	295
27 July 1937	43	124	91	—	167
7 Sept. 1937	62	97	40	—	159
20 Sept. 1937	—	—	—	—	324
16 Oct. 1937	288	315	163	—	603

Tullbergia quadrispina

Totals for depths and occasions

	α	β	γ	δ	Totals to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	54
5 May 1936	52	62	—	—	114
18 May 1936	63	85	—	—	148
28 May 1936	71	164	—	—	235
16 June 1936	67	72	—	—	139
14 July 1936	19	47	28	—	66
28 July 1936	51	55	—	—	106
27 Aug. 1936	35	63	22	—	98
16 Sept. 1936	91	99	94	—	190
15 Oct. 1936	67	65	72	30	132
11 Nov. 1936	—	—	—	—	190
10 Dec. 1936	100	63	116	84	163
13 Jan. 1937	90	58	45	0	148
10 Feb. 1937	83	119	122	—	202
10 Mar. 1937	88	130	106	—	198
7 Apr. 1937	55	72	59	—	127
5 May 1937	147	112	106	—	259
9 June 1937	50	67	25	—	117
7 July 1937	34	72	55	—	106
27 July 1937	26	87	41	—	113
7 Sept. 1937	38	65	34	—	103
20 Sept. 1937	—	—	—	—	147
16 Oct. 1937	99	82	99	—	181

Tullbergia krausbaueri

Totals for depths and occasions

	α	β	γ	δ	Totals to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	30
5 May 1936	24	8	—	—	32
18 May 1936	64	34	—	—	98
28 May 1936	49	43	—	—	92
16 June 1936	60	85	—	—	145
14 July 1936	164	93	35	—	257
28 July 1936	199	90	—	—	289
27 Aug. 1936	91	36	20	—	127
16 Sept. 1936	75	45	33	—	120
15 Oct. 1936	142	63	26	15	205
11 Nov. 1936	—	—	—	—	242
10 Dec. 1936	144	65	66	21	209
13 Jan. 1937	86	48	31	8	134
10 Feb. 1937	111	43	43	—	154
10 Mar. 1937	109	79	13	—	188
7 Apr. 1937	130	117	54	—	247
5 May 1937	76	25	10	—	101
9 June 1937	140	53	15	—	193
7 July 1937	45	14	5	—	59
27 July 1937	44	20	11	—	64
7 Sept. 1937	84	32	8	—	116
20 Sept. 1937	—	—	—	—	158
16 Oct. 1937	175	99	29	—	274

Totals for occasions, to 9 in. ($\alpha + \beta$)

	Onychiuridae	"Other Collembola"
20 Apr. 1936	195	81
5 May 1936	299	81
18 May 1936	435	373
28 May 1936	502	264
16 June 1936	641	291
14 July 1936	855	512
28 July 1936	963	505
27 Aug. 1936	726	610
16 Sept. 1936	930	338
15 Oct. 1936	1109	576
11 Nov. 1936	1126	212
10 Dec. 1936	1252	411
13 Jan. 1937	1210	193
10 Feb. 1937	1131	411
10 Mar. 1937	1200	255
7 Apr. 1937	1341	278
5 May 1937	959	239
9 June 1937	895	334
7 July 1937	793	410
27 July 1937	700	494
7 Sept. 1937	624	556
20 Sept. 1937	832	338
16 Oct. 1937	1190	684

Moisture

Means for depths and occasions

	α	β	γ	δ	Mean to 9 in. ($\alpha + \beta$)
20 Apr. 1936	—	—	—	—	52·03
5 May 1936	53·96	47·82	—	—	50·92
18 May 1936	41·58	42·78	—	—	42·18
28 May 1936	32·79	36·44	—	—	35·19
16 June 1936	45·51	41·88	—	—	43·70
14 July 1936	56·63	43·12	42·98	—	49·88
28 July 1936	49·78	37·84	—	—	43·81
27 Aug. 1936	32·20	32·05	41·06	—	32·13
16 Sept. 1936	44·65	38·91	44·26	—	41·75
15 Oct. 1936	45·01	40·13	43·61	44·75	42·57
11 Nov. 1936	—	—	—	—	52·16
10 Dec. 1936	62·15	48·99	52·68	48·53	55·57
13 Jan. 1937	62·44	49·94	52·47	52·36	54·69
10 Feb. 1937	71·88	57·55	63·05	—	64·72
10 Mar. 1937	96·34	58·16	58·41	—	77·25
7 Apr. 1937	64·60	49·09	55·11	—	56·85
5 May 1937	63·79	47·75	50·76	—	55·77
9 June 1937	45·89	40·92	47·29	—	43·40
7 July 1937	41·61	42·02	45·15	—	41·82
27 July 1937	35·55	35·55	46·00	—	35·55
7 Sept. 1937	29·05	30·60	39·59	—	29·83
20 Sept. 1937	—	—	—	—	39·53
16 Oct. 1937	35·84	44·51	43·75	—	40·17

Ignition loss

Means for depth and occasions

	α	β	γ	δ	Mean to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	12·43
5 May 1936	15·25	11·60	—	—	13·56
18 May 1936	13·80	10·70	—	—	12·25
28 May 1936	14·50	10·70	—	—	12·68
16 June 1936	13·58	10·59	—	—	12·08
14 July 1936	13·94	10·97	10·57	—	12·46
28 July 1936	—	—	—	—	—
27 Aug. 1936	13·25	10·26	9·75	—	11·77
16 Sept. 1936	13·61	10·91	9·57	—	12·26
15 Oct. 1936	13·49	10·58	9·71	8·45	12·04
11 Nov. 1936	—	—	—	—	12·67
10 Dec. 1936	—	—	—	—	—
13 Jan. 1937	—	—	—	8·30	—
10 Feb. 1937	—	—	—	—	—
10 Mar. 1937	—	—	—	—	—
7 Apr. 1937	13·55	10·78	10·46	—	12·15
5 May 1937	15·37	10·21	9·40	—	12·79
9 June 1937	14·06	10·38	9·23	—	12·22
7 July 1937	13·90	11·08	9·88	—	12·49
27 July 1937	—	—	—	—	—
7 Sept. 1937	—	—	—	—	—
20 Sept. 1937	—	—	—	—	12·06
16 Oct. 1937	—	—	—	—	—

Appendix 2. A simple soil sampler

Work on the soil may necessitate taking in large numbers samples much larger than those of the soil chemist. It is not easy to take a large sample accurately. The custom has been either to cut the sample from a large block which has been dug with a spade and brought into the laboratory (Ford, 1935) or to drive a number of iron plates into the ground to form a box from which the soil is scooped (Morris, 1922; Baweja, 1937). Both methods are laborious, and the first makes an unnecessarily big hole in the ground.

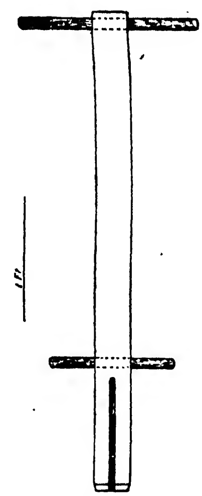


Fig. 5.

The tool illustrated takes a quick accurate sample of 8 sq. in. (51·6 sq. cm.). A sample of 8 sq. in. by 13·5 in. (34·3 cm.) deep weighs about 5 lb. (2·3 kg.). It has been successful in a heavy clay soil without many stones. It is simply a sharpened galvanized iron pipe of internal diameter 3·2 in. (8·1 cm.), this being a standard size. A half-inch slot at the lower end facilitates removal of the soil. The cutting edge is case-hardened on the inside, so that wear is differential and the edge keeps sharp. If this is not done, frequent sharpening is necessary. Holes bored through the big pipe take 1 in. pipes for the handle and foot-rail. When using it the operator stands on the foot-rail with the handle in his hands, and by wriggling rotates the sampler backwards and forwards. In this way the pipe is quickly sunk into the ground. A certain knack is required to do this, but it is very soon acquired. On withdrawing the sampler, the soil is removed by introducing a suitable instrument through the slot.

Where samples from different depths are required, the sampler is sunk to the depth of the first layer, removed and emptied, then replaced in the same hole and sunk to the

next layer, and so on. Routine samples were taken to 13·5 in. (34·3 cm.) and occasional samples to 16 in. (40·6 cm.). Deeper samples could no doubt be taken in lighter soils. For references see Baweja (1939), Ford (1935), Morris (1922).

REFERENCES

Ashby, E. (1935). "The quantitative analysis of vegetation." Ann. Bot., Lond. 49: 779–802.

Baweja, K. D. (1939). "Studies of the soil fauna, with special reference to the recolonization of sterilized soil." J. Anim. Ecol. 8: 120–61.

Blackman, G. E. (1935). "A study by statistical methods of the distribution of species in grassland associations." Ann. Bot., Lond. 49: 749–77.

Bryson, H. R. (1935). "Observations on the seasonal activities of wireworms (Elateridae)." J. Kans. Ent. Soc. 8: 131–40.

Cameron, A. E. (1917). "The relation of soil insects to climatic conditions." Agric. Gaz. Canada, 4: 663–8.

Fidler, J. Havelock (1936). "An investigation into the relation between chafer larvae and the physical factors of their soil habitat." J. Anim. Ecol. 5: 333–47.

Ford, J. (1935). "The animal population of a meadow near Oxford." J. Anim. Ecol. 4: 195–207.

Ford, J. (1937 *a*). "Fluctuations in natural populations of Collembola and Acarina." J. Anim. Ecol. 6: 98–111.

Ford, J. (1937 *b*). "Soil communities in Central Europe." [Review of Frenzel (1936).] J. Anim. Ecol. 6: 197–8.

Frenzel, G. (1936). "Untersuchungen über die Tierwelt des Wiesenbodens." 130 pp. Jena.

Handschin, E. (1929). "Urinsekten oder Apterygota (Protura, Collembola, Diplura und Thysanura)." Tierw. Deutschl. Jena, 16 Teil, 1–150.

Ingram, J. W. (1931). "Soil animals attacking sugar cane." J. Econ. Ent. 24: 866–9.

Jones, E. W. (1937). "Practical field methods of sampling soil for wireworms." J. Agric. Res. 54: 123–34.

Keen, B. A. (1931). "The physical properties of the soil." London.

Ladell, W. R. S. (1936). "A new apparatus for separating insects and other arthropods from the soil." Ann. Appl. Biol. 23: 862–79.

Maclagan, D. S. (1932). "An ecological study of the 'lucerne flea' (*Smynthurus viridis* Linn.), 1." Bull. Ent. Res. 23: 101–45.

McColloch, J. W. & Hayes, W. P. (1923). "Soil temperature and its influence on white grub activities." Ecology, 4: 29–36.

Morris, H. M. (1922). "The insect and other invertebrate fauna of arable land at Rothamsted (i)." Ann. Appl. Biol. 9: 282–305.

Park, T. (1938). "A note on the size and composition of old *Tribolium confusum* populations." Amer. Nat. 72: 24–33.

Pierce, W. D. (1931). "The bearing of the oxytofactor in insect control." J. N. Y. Ent. Soc. 39: 159–65.

Ripper, W. (1930). "Champignon-Springschwänze. Biologie und Bekämpfung von *Hypogastrura manubrialis* Tullb." Z. Angew. Ent. 16: 546–84.

Spencer, H. & Stracener, C. L. (1930). "Recent experiments with soil animals attacking roots of sugarcane." J. Econ. Ent. 23: 680–4.

Strebel, O. (1932). "Beiträge zur Biologie, Ökologie und Physiologie einheimischer Collembolen." Z. Morphol. Ökol. Tiere, 25: 31–153.

Thompson, M. (1924). "The soil population. An investigation of the biology of the soil in certain districts of Aberystwyth." Ann. Appl. Biol. 11:349–94.

SPECIAL REVIEW

RECENT RUSSIAN WORK ON COMMUNITY ECOLOGY

By J. RICHARD CARPENTER[1]

(*From the Bureau of Animal Population, Oxford University*)

CONTENTS

	PAGE
Part 1. General review	354
1. Introduction	354
2. Ecology before 1919	355
3. Post-war advances in ecology	356
4. The organization of ecological research in the U.S.S.R.	359
5. Concepts and theories	361
6. Acknowledgements	364
Part 2. Selected references	365
7. Current bibliographies	365
8. Transliteration of Russian names	366
9. References	367

PART 1. GENERAL REVIEW

1. Introduction

The purpose of this review is to offer to the student of ecology an introduction to the work which has been done in the field of community ecology in the U.S.S.R. The apparent difficulty of the language has caused an evident tendency to ignore much of the important and valuable work which has been done by Russians since the War. This is particularly to be wondered at since many of the papers have abstracts in English, German or French.

It is desirable to indicate what is meant here by community ecology. The term is not used in the restricted sense of studies of whole communities only, but to cover various aspects of synecology: the dynamics, structure, organization and functioning of biotic communities or parts of them, the interactions of the constituent species among themselves and with the habitat, and methods for their investigation. Owing to the enormously large literature involved, and for practical reasons, the plant aspect has only been discussed in connexion with the general development of ecological concepts; and the references, while often containing information about the relation of animals to plants, largely deal with animal ecology. The line drawn between synecology

[1] After the author had left England for the United States in 1938, a considerable amount of editing work was done by Mr Charles Elton, who with the assistance of Miss N. Waloff, verified from original sources most of the references given at the end of the paper. The author is entirely responsible for the paper generally, for the translations given in the text, and for those references (marked *) which could not be checked. Ed.

and autecology cannot be an exact one, and many of the papers included may be considered rather beyond the defined limits of the review, while others may have been omitted or overlooked. The inevitability of this requires no apology. Regarding the earlier time limits of this review it will immediately be recognized that the development of the community concept has everywhere been largely post-war (Shelford's *Animal Communities in Temperate America* appeared in 1913, and the work of Adams, Hankinson and Vestal *circa* 1915), and that community studies in pre-war Russia would therefore of necessity be restricted to botanical studies. The "ecological method" in the study of animals was advancing up to and through the War period; but since it has been necessary to review the biotic community work of synecology, this autecological work will have to be passed over briefly. The review, therefore, is restricted to the period since the War and up to the end of 1937. Any such review will be out of date before it is published, but it is hoped that it will at least encourage an interest in the Russian work which is being done to-day and that it may serve as a rough, though admittedly incomplete guide to the literature of the past two decades.

2. Ecology before 1919

As has been stated above, early ecological studies were largely botanical. Perhaps the earliest ecological studies were those made by foreign botanists travelling through Russia (notably von Blasius, Schrenk and Trautvetter) in the 1840's. Again in the eighties a number of accounts of Russian plant geography appeared, many in foreign languages by non-Russian authors. A bibliography of the work of this period may be found in Kuznetzov's "Uebersichten der über Russland erscheinen phytogeographischen Arbeiten" (1898, etc.). There is also an account by Batalin (1881): "Aperçu des travaux russes sur la géographie des plantes de 1875–1880." The *Humboldt Centarschrift* (Gesellschaft für Erdkunde, Berlin), 1899, should also be consulted in this connexion. It is noteworthy that these earlier studies, done before the full impact of the Darwinian influence on scientific research had occurred, had little to do with the later revival of ecology as we know it to-day. However, plant ecology developed towards the turn of the century, as is indicated by the publication of the Russian translation of Warming's *Plantesamfund* (*Oecology of plants*) in 1901, eight years before its translation into English. Other indications of its development were the surveys—largely ecological—which were conducted by Fedchenko and published by the Ministry of Agriculture, of the sparsely populated areas of Siberia and the Far East, undertaken with the idea of organizing planned emigration of peasants from the overcrowded areas of European Russia. Plant ecologists of the pre-War period who should be mentioned are, in addition to Fedchenko: Alekhin, Elenkin, Il'inskii, Korzhinskii, Kuznetzov, Morozov, Pachosskii, Ramenskii, Shenikov, and Sukachev.[1]

[1] For a comment on the method of transliteration of Russian names, see p. 366.

Animal ecology prior to 1919 was, strictly speaking, autecology (as was largely the case elsewhere). Notable exceptions were N. A. Severtzov's two publications, *Periodic phenomena in the life of the mammals, birds and reptiles of the Voronezh District, based on observations during* 1844–53 (1855), and *The vertical and horizontal distribution of the animals of Turkestan* (1879). Some beginning of ecological observations had been made previously by Nordmann (1833) in south Russia, by Baer (1839) on Novaya Zemlya, and by Middendorff (1875) in northern and eastern Siberia. In the works of Eversmann (1840) for the Aral-Caspian basin, of Menetrié (1850?) for the Caucasian mountain altitudinal zones, and of Chernai (1853) for the Kharkov Government, we find lists of animals to be found in various habitats or stations (statio). Chernai and Severtzov were both influenced in their studies by the lectures (published in 1852) of Rule, who emphasized the need for studying associated plants and animals in relation to their surroundings. Apparently Rule's recommendations had but little further effect until very recently in the encouragement of ecological study. The early "ecological" studies were to some extent zoogeographical, but Russian zoogeography had its modern beginning with the works of Menzbir (*Ornithological geography of European Russia*, 1882; *Zoogeographical atlas*, 1912). It is interesting to note that Kobelt's *Die Verbreitung der Tierwelt* was translated into Russian in 1903, and Scharff's *European animals* in 1918. Hydrobiology had for some time been studied fairly intensively (see Zernov, 1921): the many lakes of the glaciated portion of Russia as well as the larger southern ones offered many opportunities for this type of investigation; the names of Deryugin and Zernov should be mentioned in this connexion. The work was both faunistic and limnological, probably being influenced to some extent by the German research in fresh-water biology which was done during the latter portion of the nineteenth century.

3. Post-war advances in ecology

The recognition of the biotic community concept in Russia was apparently first made in hydrobiology. Its application to terrestrial studies was pointed out by Alpatov (1923) in a paper reviewing the American work of Shelford and Adams and their associates and giving a general account of the aims and methods of ecology. Shortly after this date, Alpatov went to America as a research fellow of the International Education Board and worked for several years on *Drosophila* at Johns Hopkins University. His association at Johns Hopkins with Pearl is reflected in one of Alpatov's students, Gause. In 1923 Dogel began the publication of a series of studies on the fauna of individual plants and of vegetation strata, which was supplemented by Vladimirskii and other associates. In 1924 Beklemishev began the direction of a series of studies at the Biological Station of the University of Perm, and a number of interesting publications on community ecology by him and his students began

to appear. Kashkarov had been influential in instigating and encouraging ecological work, and in 1928 visited a number of institutions in America; on his return he initiated the *Journal of Ecology and Biocenology*, which was later reorganized to appear as a yearly publication, *Problems of Ecology and Biocenology*. The extension of community methods about 1929–30 to the acute locust problem, which was already advanced in the methods of autecology, contributed to the rapid advance of synecology (or "biocenology", as it is termed in Russia and elsewhere on the Continent); names which are especially important in this connexion are Bei-Bienko, Ivanov, Nefedov, Predtechenskii, Rubtzov, and Vinokurov, in addition to many others. While there is no adequate review of the extensive work on locust ecology, the bibliographies in the works of Uvarov (*Locusts and Grasshoppers*, 1931) and Predtechenskii *et al.* (1935) are fairly extensive and give an introduction to the copious literature on the subject.

Kashkarov gives the following account (translated from Kashkarov, 1937*b*, pp. 214–15) of the growth of Russian ecology:

> The extent of ecology in the U.S.S.R. before 1930 may be seen in the *Proceedings* of the Congresses of Zoologists. Already in the first Congress, held in December 1922, ecology had an official place in the ranks with systematics and zoogeography, which it had not had in the previous Congresses of Naturalists. Of the 29 papers in the section of Systematics, Ecology and Zoogeography, seven were ecological. Co-ordinated with this section was the section on Hydrobiology, where there were about 10 papers of an ecological character. In the second Congress (May 1925), of 46 papers in the section of Systematics, Ecology and Zoogeography. 12 were ecological, a series of ecological papers were presented in the section on Hydrobiology, and, finally, in this congress there were seven sections dealing with applied zoology, some of their papers having an ecological character. The third Congress (December 1927) had ecological papers of a general character read in the plenary session (by Beklemishev, Kashkarov, Dembovskii and Pavlovskii), and a series of papers on ecology in the section of systematics, ecology and zoogeography. Even a greater number of ecological papers were read in the fourth congress (May 1930), both in the general assembly and in the usual section. Also, there was passed a resolution on ecological topics, regarding the indispensability of the ecological study of economic animals and the necessity of work on the methods of collecting quantitative data, etc.

In addition to the four meetings of the All-Union Congresses of Zoologists mentioned by Kashkarov, several other assemblies should be mentioned, namely, the All-Ukrainian Zoological Conference held in 1931,[1] Botanical Congresses held in 1926 and 1928, and a Hydrobiological Congress in 1930. There was an Anti-Plague Conference in 1927, and there have been many others on various topical subjects (e.g. on specific injurious rodents, etc.) which have been held from time to time. Several discussion groups have been organized at Leningrad, Moscow and Voronezh; the two discussions reported in *Soviet Botany* (1934, No. 3 and No. 5) were held in the Leningrad Botanical Institute under the auspices of Keller and Kashkarov; both botanists and

[1] J. Cycle Bio-Zoologigue, 1–2: 105–20. *Ug.*

zoologists were represented. The meetings of the Ecological Committee of the Leningrad University Society of Naturalists are reported in *Problems of Ecology and Biocenology*.

Ecology has begun to be taught in the universities: in 1924 there was begun a course in ecology at the Middle Asiatic State University (Tashkent) by Prof. D. N. Kashkarov, in 1925 by I. Strel'nikov in the Leningrad State University. In the University of Moscow there is a course by Prof. Alpatov, in Smolensk and later at Kharkov by Prof. V. Stanchinskii, in Voronezh by Dotzent Konakov, etc. Besides courses in general zoology in Leningrad there is also a course in experimental ecology. There is also given in a number of universities a course in the ecology of plants (by Korovin in Tashkent, Poplavskaya in Leningrad, etc.). Work is not organized wholly by courses; in a number of universities and institutes there have been organized laboratories of ecology: in the Leningrad State University, in Moscow State University (the first Russian ecological laboratory, founded in 1931); in the Peterhof Biological Institute of the Leningrad State University there is organized a laboratory of experimental ecology; also, there are the laboratories of the Leshaft Institute and the laboratory of ecology organized by the Zoological Institute of the Academy of Sciences, the All-Union Institute of Plant Protection, the Institute of Hybridization and Steppe Acclimatization in Ascanya Nova, the Scientific Research Institute in Kharkov, the Institute of Zoology and Biology of the Ukrainian Academy of Sciences, the Middle Asiatic University, the Uzbekistan Institute of Experimental Medicine, etc. (Translated from Kashkarov, *loc. cit.*)

A note should be added as to the general method of carrying out investigations. The development here may be roughly divided into two periods of a decade each. During the first period many expeditions were sent throughout the country collecting data and material. "Much material was collected by these expeditions, in post-revolutionary times the network of their paths covering even the most remote and inaccessible parts of the country." (Translated from Formozov, 1937*c*, p. 928.) Men important in the directing of these expeditions and the processing of material after their return were Ognev, Vinogradov, Geptner and Bobrinskii, among many others.[1]

These expeditions sometimes gave valuable material on the geography but only partly on the ecology of mammals. In the collecting parties there are now included numerous hunters and amateur naturalists who often are able to kill masses of material for this or that problem. The second decade of investigation was the period characterized by the rise of a number of biological stations and the transition from the expedition as a method of work to one of utilizing stations....The zonal organization of stations for the investigation of the ecology of economic animals is an unbroken complex network of state Preserves of Natural Conditions....The introduction of biological stations in preserved areas, the observation from various points by the Administration of the North Sea Passage and the filial organizations of the U.S.S.R. Academy of Sciences have made it possible in recent years for Soviet ecology to determine rapidly a series of important theoretical and practical problems. (Translated from Formozov, *loc. cit.*)

[1] The more recent expeditions which have been supervised and sent out by the Zoological Institute of the Academy of Sciences are discussed by Pavlovskii, 1937.

4. THE ORGANIZATION OF ECOLOGICAL RESEARCH IN THE U.S.S.R.

The organization of science in the U.S.S.R. is entirely a part of the government organization and has its purposes defined in each five-year plan (*pyatiletka*). The government of the U.S.S.R., the All-Union Congress of the Soviets, does nearly all of its administration through the Central Executive Committee (TZIK). Scientific organizations in the several republics not included in the R.S.F.S.R. (e.g. the Turmen S.S.R., the Ukrainian S.S.R., the Armenian S.S.R., the various Caucasian republics, etc.) are, strictly speaking, not responsible to the TZIK, but inasmuch as all are, in the last analysis, responsible to the All-Union Congress, close co-operation and similar organization are carried out.

So far as ecological research is concerned, there are three essential bodies in the U.S.S.R. with which we are interested: the Academy of Agricultural Sciences, the Academy of Sciences and the Committee for Higher Technical Education, in addition to the organizations of the individual republics which will be mentioned later. The Lenin All-Union Academy of Agricultural Sciences (also sometimes called the Agrarian Institute; literally, in Russian, the "All-Union Academy of Agricultural Sciences named after Lenin") has as one of its institutes the Institute of Plant Protection (also sometimes called the Institute of Pest Control), VIZRa, where most of the ecological work of this Academy is done. The more recent work and the present problems being considered may be found discussed in an article by Rainey (1938). The Academy of Agricultural Sciences was, until 1935, a part of the late Communist Academy (before 1926 termed the Socialist Academy).

The All-Union Academy of Sciences of the U.S.S.R. has a long history, having been founded by Peter the Great in 1724–5. It maintained its essential organization of the pre-revolutionary period until about ten years after the revolution, when it was reorganized. There are 93 active members, only a small proportion of whom are party members; it also has about 68 honorary members and about 300 corresponding members. While various authorities give various compositions of the membership of the Academy, there being no doubt some changes from time to time, the following figures give a representative idea of the membership in, at least, 1935: Mathematics, 4; Physics, 8; Technics, 18; Chemistry, 10; Geology, 8; ***Biology***, 13; History, 6; Social Economy, 6; European Languages and Literatures, 10; Orientology, 8; Philosophy, 2. The Academy is divided into three great departments, those of Sociology, Technics, and Natural and Mathematical Sciences. The latter department is divided into what are known as "associations" of sciences: the physico-mathematical association, the geological association, the chemical association, and the biological association. Included in the latter are the following institutes and laboratories, located either in Moscow or Leningrad: the Institute of Genetics, the Palaezoological Institute, the Physiological Institute, the Laboratory of

Microbiology, the Laboratory of Biochemistry and the Physiology of Plants, a similar laboratory for animals, the Institute for Forest Research, the Laboratory of Zöogeography, the Laboratory of Experimental Zoology and the Morphology of Animals, the Botanical Institute and the Zoological Institute; it is in the last four that most of the ecological work is done. Certain biological stations are also attached to the Academy of Sciences, e.g. the Sevastopol, Baikal and Khibin stations.

The Academy itself was officially transferred to Moscow in 1934, but there is still a branch ("filial") in Leningrad; other filial organizations may be found in various places throughout the U.S.S.R., e.g. in the Urals, Tajakstan, Azerbad, Kazakstan, Transcaucasia, Vladivostok, etc. (There are also Academies of Science in Ukraine and in White Russia.) Co-ordinated with these filials there are a number of "bases" which are used as more or less temporary stations for many expeditions, and which sometimes later may become permanent stations or filial organizations. Examples of these bases are those in Tajakstan, Kol'sk, and the polar bases. The filials usually have several institutes of biology, geology, chemistry, and the Far-Eastern Filial at Vladivostok has a fresh-water biological station, the Kedrovaya-Padi preserve, and a seismic station as well.

Certain other biological stations are under administrations other than the Academy of Sciences; for example, the Arctic Institute (formerly the Institute for the Scientific Exploration of the North) is under the direction of the Chief Administration of the North Sea Route, the Kossino Limnological Station is under the Moscow-Kazan Waterway Commission of the Hydrometeorological Administration, the Azov-Black Seas Scientific Fisheries Station and the State Oceanographic Institute (Moscow) are under the Department of Food Industry, and the Institutes for Microbiology and Epidemiology at Rostov-on-Don and Saratov are under the Public Health Department. Other stations are controlled by the Universities and Societies of Naturalists: the Peterhof Science Institute is run by the Leningrad State University; the Murman Biological Station (at Alexandrovsk) by the Leningrad Society of Naturalists; the Zvenigorod Hydrophysiological Station by the Zoological Institute of the University of Moscow; the Bolchevo station by the Society of Friends of Natural Science, Anthropology and Ethnology; the Kama Biological Station by Perm University; a bio-station by the Gorky (Nizhni-Novgorod) State University; and the Donetz Biological Station by Kharkov University. There is also a wide network of State Preserves, each usually having a station. Preserves which may be mentioned are the Chapli Steppe Preserve (under the Ukraine Academy) at Askanya Nova, the Crimean Preserve at Aluishita, the Azov-Sivash Preserve, the Caucasian and Astrakhan Preserves, the Volga-Kiev Preserve at Pensa, the Smolensk Forest Preserve, the Kedrovaya-Padi, Sikhote-Alin and Khibin Preserves in the Far East, the Izmailovsk Preserve near Moscow, the Lapland Preserve, the Naupzumsk, Tajakstan, Voronezh and Kursk

Preserves, in addition to many others which have not been so well studied. Other biological stations which should be mentioned are the Arnoldi Station at Novorossisk, the Borodin Station at Leningrad, the Volga-Kama Station, the Novosibirsk Station, the Kertch Limnological Station in the Crimea, the Karadagsk Station, and the Turkemhistan Zoological Station.

There are also several institutes of interest which have not yet been mentioned: the Tropical Institute (Moscow and Uzbekistan), the Subtropical Institute at Tashkent, the Pacific Institute of Fisheries and Oceanography at Vladivostok, the Zoological Gardens at Moscow and Novosibirsk, the Solovetzk nursery, the Nikitsk Botanical Gardens, etc., where ecological observations are made on animals and plants. Probably most important of all, however, are the ecological laboratories in the various institutes of zoology, biology and botany at the universities at Leningrad, Moscow, Perm, Voronezh, Tashkent, Kharkov, etc.

When plotted on a map of Russia, these stations, preserves, laboratories and institutes cover very well indeed the European part of the Union as well as "Middle Asia" and the Far East, although there appears at present to be a gap in the central portion of Siberia. The work done by these various institutes may be judged by the fact that a number of them issue their own publications to which references are made in the bibliography.

5. Concepts and theories

The Russian concepts of biotic community ecology are somewhat different from those of the Scandinavian and American schools of thought, although adherents to both these may be found. The precise meaning of the term "biocenology", together with the underlying ideas of the Russian ecologists, may perhaps best be conveyed by citations from the translated conclusions of several important papers dealing with the question. These are cited here because such important reviews of ecological thought as Phillips' in the *Journal of Ecology* (1931, 19: 1–24) have included no reference to the Russian concepts. Most of the citations below have been made by translation. It will be noted that the biotic concept had its origin in Russia in connexion with hydrobiological studies.

Filip'ev (1924): The term "biocenosis", introduced to science by Möbius (1877), is often met in the Russian hydrobiological literature into which it was introduced by Zernov in 1912, but various authors have employed it in very different senses. The purpose of this note is to propose an exact terminology which will be able to minimize confusion.

1. Facies: the lithological properties of the sea bottom. The organisms are able to inhabit the sea bottom, but it is only their inorganic parts which contribute to its formation.

2. Station: a part of the sea bottom which, due to similar physico-chemical conditions, bears similar faunas.

3. Biocenosis: the sum total of the constant population of a stratum, without taking into account the special relations of the organisms between themselves or to the substratum (i.e. the "animal community" of Petersen).

4. Association: a group of organisms united by conditions of existence, by plants, animals, or only by the substratum.

5. Ecological group: an assemblage of organisms with one ecological parallel: herbivores, planctonivores, leaping forms, swimmers.

Ecological analysis of the benthos may go in two directions: centrifugally—the physiological study of separate forms—and centripetally—a division into proposed groups. The second method reduces the complexity of the population of the sea and permits of an easier orientation.

The biocenosis has every right to be studied for itself, all the more since it is the only basis which conveys to us the significance of the organization of the sea. It is the only means of having this rich material contribute to the analysis of the great problem of the general economy of sea life.

Resvoi (1924): A biocenosis is a dynamic state of equilibrium maintaining a population-system, this equilibrium arising under given ecological conditions.

From Möbius's representations it is clear that the biocenosis is, above all, a versatile or dynamic state of equilibrium. In biology the presence of a "system of dynamic equilibrium" [bewegliche Gleichgewichtssystem] was first designated by Elenkin in 1921. The "ecological conditions" should be understood to mean the sum of the influences, both the conditions of outer existence and the element of the continuity of life or of organisms, which populate the habitat [Lebensraum] concerned. In short, all conditions which represent the environment of the given biocenosis. The habitat of the biocenosis—all parts of it, biologically speaking—must likewise be of equal or similar conditions. Such a habitat is meant by the designation "biotop" (Dahl, 1903–21), or "statio" [=station] (Vereshchagin, 1914; Filip'ev, 1923). Both designations are wholly identical in their meaning.

From the above it follows that the biocenosis is composed by the population of the biotop. Between the properties of a given habitat and its population (i.e., between a biotop and its biocenosis) a functional connexion is always present. For each environmental variation [Milieu-Veränderung] there will be a corresponding resultant in the population; each variation in the population (e.g. through the activity by man) must call for a corresponding result in the variation of the environment.

Only to a certain point is a biocenosis a self-sufficient and strongly contained system: the biocenotic relationships go beyond the boundary of the biocenosis, and the boundaries of a biocenosis in water depend on the articulation of these latter interrelationships.

Beklemishev (1931) ["The organism and the biocenosis"]: One of the most important questions of biocenology is the following: May the natural communities of organisms be considered as organic individuals or organisms and in what degree? It is wholly a mistake to implicate the criterion of individuality in the diagnosis of communities or, on the contrary, to eliminate it for *a priori* reasons. The question of individuality of each biological object must on each occasion be answered inductively. And it is necessary for us to be clear in each individual case what we mean by a "living individual", "organism", or "community" (Gesellschaft, biocenosis, etc.).

Organization is the chief criterion of an organism....If the conceived system possesses the criterion of having its living parts regulated so as to form a constant, we may then speak of an organism; it would be better to speak of a higher degree of organization, since most (or all) organisms are composed of parts each of which in their turn have an unquestioned individuality. And to understand the social structure of every organism we must prove the degree of individuality of each part itself, i.e. all valid regulatory mechanisms which are exhibited and which are maintained by the specific structure and the specific functions of the given part. Corporeal continuity is, on the other hand, not a necessary criterion of the organism, any more than the origin (through aggregation or differentiation).

The Biocenosis. Plant sociology is in possession of a great arsenal of concepts concerning the distinction between the different types of plant communities, and if the botanists are still far from agreement among themselves, there are certainly several concepts which are apparently generally acknowledged. Among the zoologists the Americans are using the botanical terminology most, and are correct in so doing. The Western Europeans and the Russian zoologists and hydrobiologists employ as a rule one single expression: the biocenosis. Their meaning of the biocenosis is thus the same as that of the early concept of the "plant association" of the 1910 Botanical Congress in Brussels, which expresses the meaning of the word biocenosis as it is generally used in the literature to-day, be it used in the abstract or concrete sense.

It appears to me that most definitions have not adequately described the content of the biocenosis concept. From Möbius up to Resvoi we find more and more concepts being introduced into the biocenosis concept, as if it were a strong storehouse of concepts. Our first task is to study the structure of the life covering the earth and to designate the natural constructive rankings. As logical outgrowths of this we shall study (1) the biocenotic units or cenoses and their interrelationships, and (2) the sociological significance within the cenoses (regulatory mechanisms, the functioning of the equilibrium, etc.). We will obtain, so to speak, an anatomical and histological analysis of the geomerid,[1] the life clothing the earth. We must state from which constructive unity and by what manner this covering of the earth is put together, and then investigate to which of these unities and in what degree the definitions of Möbius, Vereshchagin or Resvoi correspond.

Beklemishev criticizes the

artful partition of populations of organisms of every habitat [Standort] in a phytocenosis, and the superimposing of a higher taxonomic category of the Linnean system on it without meaning. "Life forms" and "basic forms" [Grundformen], not kingdom and class, should be applied to the biocenotic distribution of organisms." [The concepts of the continental plant sociologists (whose emphasis is upon small "synusia") are considered as insufficient to cope with biotic phenomena.] Among the organisms one can always find in similar layers and aspects of a cenosis animal species which live in neighbouring growths with the same plants and with different animals. A common view of plants and animals would complicate the present methods and concepts of plant sociology very much. The question of stratum existence of motile animals, for example, includes a difficulty which is wholly unknown to the phytosociologists. Periodic or unperiodic migrating animals complicate the question of the time aspects of communities. Larger animals often belong to the larger biocenotic units without having attachment with the smaller; for example, in the Kama lowlands the hare belongs to a known meadow complex and has no relation [Verbindung] with plant associations belonging thereto.... We must leave the "association concept" of the plant sociologists to them, and stand by the biocenosis concept of the zoologists....

That the biotic concepts of Beklemishev are not held by all Russian ecologists is indicated by the work of Sukachev (1918), a plant ecologist adhering to the ideas of the Swiss school of ecology:

A phytocenosis is the sum total of a given territory organized through the struggle for existence among the dominant plants with the conditions of the habitat [Standort], and characterized by the given mutual relations of the plants to one another as well as to their habitat.

A plant association or "phytocenosis type" is essentially uniform through the struggle for existence competition and corresponds to the habitat relations of organized phytocenoses.

[1] Expressed by K. D. Starinkievich, who designated the sum total of life as the highest biocenosis, as would be meant by terming the biosphere the highest biotop (Vernadskii, 1926).

Therefore it is accommodated equally throughout to the moisture requirements for existence, i.e. phytocenoses which have essentially similar species lists, structure, and composition of the distinguishing synusia of which they are constructed. External physiognomy and biological uniformity through a similar complex of communities enable the formulation of the influential factors of habitat conditions.

A practical view of the purposes of ecology is taken by Bukovskii (1935) who considers that the Americans place undue emphasis on the details of biotic succession and finds it a "fatalistic" phenomenon,[1] the Western Europeans place too much emphasis on structure [cf. the view of Beklemishev above], and the hydrobiologists too much upon the equilibrium and the balance of populations:

The basic aim of biocenology is to study the laws that govern the dynamics of biocenoses and to regulate their quantitative and qualitative content, and, having obtained strictly scientific data, to produce the alterations in the composition of biocenoses that we find desirable.

Minin (1936): The station is a unit of the arena of life, characterized by a complex of edaphic, biotic and climatic factors, more or less separated from the neighbouring units of the same life-zone, and still more from those of different life-zones. [See comment of Shelford which follows.]

The term "biotop" must be looked upon as synonymous with the term "station"; it also is a division of the space of life. The term "habitat" is employed by most ecologists in the same sense. The term "habitat" must be related not to space but to species. The habitat is the complex of ecological conditions necessary for the evolution of the complete life-cycle of a species population. The habitat of a species can include many biotops (or stations) and in one biotop can be many habitats.

Veitzman (1936) cites the use of the term "constation" as including all of the "stations" occupied by an organism, but criticizes its being applied to all habitats occupied during the entire life-history of such migratory organisms as certain birds.

As a closing word in considering Russian ecological concepts, an óbservation of Shelford (1934) should be reiterated: the "life zones" described by Filip'ev (1929*b*), Kashkarov (1927)[2] and Kashkarov & Korovin (1931) are based on the natural vegetation regions and hence are not comparable to the so-called "life zones" of Merriam and others for North America which are based on temperature summation. The use of similar terms here is unfortunate.

6. Acknowledgements

I wish to thank the following for their assistance in the preparation of this review: Prof. V. V. Alpatov for information regarding the earlier development of post-War Soviet research in animal ecology, for his interest and courtesies during my recent visit to the Ecological Laboratory at the University of

[1] There is no way of knowing how widely this view is held, but the scarcity of papers dealing with biotic succession may be pointed out; those of Plyater-Plokhotskii (1936) and Bei-Bienko (1936) are notable exceptions.

[2] ["An ecological study of the environments of Lake Sarg-Tshilek, North Ferghana."] Turkestan. *Rg.*

Moscow, and for his suggestions during the preparation of the manuscript; Prof. D. N. Kashkarov and Prof. A. N. Formozov for copies of several papers summarizing certain phases of Soviet ecological work; Prof. A. C. Hardy of University College, Hull, for information about certain Russian publications on oceanography; and Dr B. P. Uvarov for suggestions and criticisms. I am particularly indebted to Mr Charles Elton for the editorial work he has done on this paper (see footnote on p. 354), and to Miss N. Waloff who assisted him in checking references; also to Mr Elton for advice and for the use of the Russian publications in the Bureau of Animal Population. I also wish to thank the library staff of the Imperial Institute of Entomology and the British Museum (Natural History) for their assistance in making available many publications.

While I am indebted to all these people for various services, it should be pointed out that the opinions expressed in the text, unless indicated as quotations, are entirely my own, and for them I alone am responsible.

PART 2. SELECTED BIBLIOGRAPHY

7. Current bibliographies

As mentioned in the introduction to Part 1, any guide to current literature will be out of date before it is published. The most that can be done to remedy the situation, therefore, is to suggest the generally available means of keeping informed concerning the large amount of Russian ecological literature which is now being published. The bibliography in this Part includes a number of summaries of work on various subjects not included in this review; 1937 was a "peak year" for summaries of this type, it being the twentieth anniversary of the Revolution.

Other publications which help one to keep abreast of the current literature are the especially valuable *Miscellany* (or "*Abstracts of the Works of*") *the Scientific-Research Institute of Zoology of Moscow State University* (which contains summaries and bibliographies of the work done in its various departments); *Problems of Ecology and Biocenology* (which contains, in addition to many ecological papers, a "chronicle of ecological investigation in the U.S.S.R." and the proceedings of the Ecological Committee of the Leningrad University Society of Naturalists); the *Summary of the Scientific Research Work of the Institute of Plant Protection* (1935 edition being summarized in English in the *Rev. Appl. Ent.* A, 25: 137–60); and the *Bulletin of the Arctic Institute*[1] (which contains many notes and bibliographies of publications, both Russian and foreign, relating to investigations in the Northern Regions). A section entitled "Bibliographia hydrobiologica rossica" appeared in each number of the now extinct *Russkii Hydrobiologicheskii Zhurnal* (i.e. up to 1930), and included bibliographies in Russian and English/French/German on all papers dealing with Russian hydrobiology.

In addition to the above Russian publications, the following also frequently

[1] Now no longer issued, being partly replaced by *Sovetskaya Arktika*.

contain references to Russian ecological work: *Biological Abstracts*, the *Zoological Record*, the *Berichte über wissenschaftliche Biologie*, the *Review of Applied Entomology*, the *Tropical Diseases Bulletin*, and the *Journal of Mammalogy*.

Beginning with the 1936 publications, the Russian zoological literature is being collected by the Library of the Zoological Institute of the Moscow State University under the direction of Prof. V. V. Alpatov, and will be sent to the *Zoological Record*. The 1936 references appeared in full (in Russian) in the *Zool. Zh.* (1937), 16: 1022–77.

The Library of the Bureau of Animal Population, Oxford, has a growing collection of Russian reprints and some journals, and has had translations made of some papers. Copies of these translations can be purchased from the Bureau of Animal Population, University Museum, Oxford.

8. Transliteration of Russian names

The transliteration of names from the Slavonic (Cyrilic) into the Roman alphabet creates a certain amount of inevitable confusion, caused chiefly by the fact that English, French, and German authors each transliterate names into their own language on a phonetic basis. The generally accepted English criterion, that used by the British Museum, the *Review of Applied Entomology*, and in the transliteration of Slavonic names on to British maps, is given below. For reasons of bibliographical convenience I differ from this system in not printing the ĭ with its accent. The greatest confusion arises with the labial and sibilant consonants, and this reaches a climax when these elements occur at the beginning of a name, since it causes a change in the alphabetical arrangement of the bibliography. Included in parentheses after the approved equivalent are substitutions frequently found in the French and German literature. The use of these foreign equivalents is not "wrong", but the adherence to one standard in English publications seems desirable and convenient.

Russian	English	(Other)	Russian	English	(Other)
А, а	*a*		П, п	*p*	
Б, б	*b*		Р, р	*r*	
Ч, ч	*ch*	(*tsch, tsh, č, tch*)	С, с	*s*	
Д, д	*d*		Ш, ш	*sh*	(*sch, š*)
Е, е	*e*		Щ, щ	*shch*	(*šč, ch*)
Э, э	*é*	(*ė**)	Т, т	*t*	
Ф, ф	*f*		Ц, ц	*tz*	(*ts*)
Г, г	*g*		У, у	*u*	(*ou*)
I, i	*i*		ы	*ui*	(*y*)
И, и	*i*		В, в	*v*	(*-ff, -w*)
й	*i* (*ĭ*)		Я, я	*ya*	(*ja, ia, i͡a**)
К, к	*k*		ѣ	*ye*	(*je, e, i͡e**)
Х, х	*kh*	(*ch*)	Ю, ю	*yu*	(*ju, u, i͡u**)
Л, л	*l*		З, з	*z*	
М, м	*m*		Ж, ж	*zh*	(*j, sh*)
Н, н	*n*		ь	'	(frequently omitted)
О, о	*o*		ъ	‘	

* These forms frequently found in American literature.

Frequently names ending in *-iĭ* are spelled *-y* (e.g. Brodskiĭ, Brodsky); with but very few exceptions, names ending in *-ow* and *-off* should be *-ov* in English (e.g. Formozov, Kashkarov, etc.).

9. REFERENCES

The following list of 517 references is not intended to be a complete bibliography of Russian ecological work, or even of work dealing with community ecology in the sense used in this review. It is meant to give a guide to some of the main trends of this research, with emphasis rather on papers that contribute to ecological theory and method, rather than to purely economic or *ad hoc* research. It should be stated, however, that Soviet theory identifies general ecology with its application to the uses of mankind, and that there is a very large literature on special economic biological and epidemiological problems of which it has been impossible to give more than an indication here. A great deal of this literature contains valuable contributions to community ecology.

The omission of particular papers is explained partly by the accidents of library organization (Russian literature is not yet completely available in this country), and partly by reasons of space. On the whole it was thought to be preferable to give only those references which could be actually verified. In the case of certain papers of obvious importance this rule has been relaxed. The large number of reviews of Russian research published on the occasion of the recent twentieth anniversary of the Revolution provides good bibliographies in Russian to many of the subjects.

The titles given within square brackets are usually those of the summaries in non-Russian, modified sometimes to give a better sense of the original title. The titles of papers without non-Russian summaries are taken (or modified) in the same way from the table of contents in non-Russian, or else translated from the original. Authors' names are transliterated directly from the Russian; when this transliteration deviates from the version usually found so much as to cause confusion, the commonly found form is added in square brackets. Work bearing on Russian ecology not done by Russian workers, but of interest here, is indicated by the symbol §.

Certain publications have not been seen by me, and it is possible that they have translated summaries in non-Russian; these are indicated by the symbol ♯ after the abbreviation which shows the language the paper is written in. For this purpose the following abbreviations are used, a capital letter indicating the text of the paper, a small letter the summary in another language: *R*, *r*, Russian; *E*, *e*, English; *F*, *f*, French; *G*, *g*, German; *U*, *u*, Ukrainian.

The abbreviations for the periodicals mainly follow the system of *World List of Scientific Periodicals* (1934), but many journals are not in this *List*, while in the case of others it has been found desirable to use a different

abbreviation. The figure before the colon indicates volume (or number, where this is used, as frequently in U.S.S.R., in the sense of volume); the figures after the colon indicate pages. The number (in the ordinary meaning of subdivisions of a volume) is usually omitted from these references. But where, as is not uncommon, the paging starts afresh with each number, the number is included in round brackets before the colon. This practice of paging numbers separately appears to be dying out, but it adds to bibliography a complication of which the reader should take note.

[*Editor's Note.* As mentioned in the footnote on p. 354, the majority of the references have been checked from the original sources by Mr Charles Elton and Miss N. Waloff. Those which could not be checked, and for which the author is therefore responsible, are marked with an asterisk. The symbol † indicates that a translation is available in the Bureau of Animal Population.]

*__Alechin, V. V. (1925?).__ "Ist die Pflanzenassoziation eine Abstraction oder eine Realität?" Bot. Jb. 60, Beibl. 135: 17–25.

Alechin, V. V. (1931). ["Les steppes russes et les méthodes d'investigation de leur tapis végétal."] Bull. Soc. Nat. Moscou, Sect. Biol. 40: 285–383. *Rf.*

*__Alpatov, V. V. (1923).__ ["Ecology, a trend in regional studies in zoology."] Kraevedenie: 26–30. *R.*

Alpatov, V. V. (1933). ["The work of the Ecological Laboratory in 1931."] Miscellany Inst. Zool. Moscow St. Univ. 1: 7–21. *R.*

Alpatov, V. V. (1934). ["The density of population as an ecological factor."] Advances Modern Biol. 3: 229–51. *R.*

Alpatov, V. V. (1935). ["The work of the Ecological Laboratory in 1932."] Miscellany Inst. Zool. Moscow St. Univ. 2: 84–7. *R.*

Alpatov, V. V. (1935). ["The Ecological Laboratory of Moscow State University and its work in 1931–1934."] Advances Modern Biol. 4: 533–9. *R.*

Alpatov, V. V. (1936). ["The work of the Ecological Laboratory in 1933."] Miscellany Inst. Zool. Moscow St. Univ. 3: 171–5. *Re.*

Alpatov, V. V. (1937). ["The zoological scientific literature in the U.S.S.R. on the eve of the 20th anniversary of the Revolution."] Zool. Zh. 16: 783–90. *R.*

*__Andreev, V. N. (1933).__ "Die Tundren-Unterzonen des nordeuropäischen Teiles der U.S.S.R." Bot. Jb. 66: 119–27.

Andreev, V. N. (1935). ["Vegetation and natural zones of the eastern part of the Bolshezemlskii Tundra."] Rep. Polar Commission Acad. Sci. U.S.S.R. No. 22: 1–97. *R.*

Andrushko, A. M. (1936). ["Methods and technique of the census of reptiles in deserts."] Probl. Ecol. Biocenol. 3: 158–67. *Re.*

*__Anon. (1926).__ ["Übersicht über die Stationen (1921–1925)."] Bull. Oceanogr. Inst. Moscow, 1: 75–81. *R.*

Anon. (1931). ["Catalogue of literature about injurious insects in U.S.S.R. in 1925–28."] Leningr. Acad. Agr. Sci., Inst. Pl. Prot. 95 pp. *R.*

Anon. (1935). ["Chronicle of ecological investigations in the U.S.S.R."] Probl. Ecol. Biocenol. [2]: 250–6. *Re.* (And similar articles in later volumes.)

Arnol'di, L. V. & Fortunatova, K. R. (1937). ["On groupings of littoral fishes in the Black Sea according to the biology of feeding."] Zool. Zh. 16: 773–6. *Re.*

*__Atztzi, D. (1932).__ ["Agricultural ecology."] Moscow. *R.*

Baer, K. E. von (1839). "Schilderung des thierischen Lebens auf Novaia Zemlia." Arch. Natur, 5 (1): 160–70.

Baranov, V. (1933). ["Notes on the symbology of a geobotanical map."] Bull. Inst. Rech. Biol. Perm, 8: 277–82. *Re.*

Baranov, V. & Bei-Bienko, G. (1926). ["Über eine phyto-ökologische Charakteristik der Standorte der saltatoren Orthopteren in Altai."] Bull. W. Sib. Geogr. Soc., Omsk, 5: 179–98. *Rg.*

***Bartenev, A. N. (1930).** ["Materialien zur Kenntnis der Odonaten-Fauna von West-Kaukasus."] Proc. N. Cauc. Ass. Sci. Res. Inst. 72 (14): 1–138. *Rg.*

Baskina, V. & Fridman, G. (1928). ["A statistical investigation of the animal components of two associations in the Kama flood plain."] Trav. Inst. Rech. Biol. Perm, 1: 183–295. *Re.*

***Batalin, — (1881).** "Aperçu des travaux russes sur la géographie des plantes de 1875–1880." 3. Int. Geogr. Congr.

Behning, A. (1927). "Die hydrobiologischen Forschungen in der U.d.S.S.R." S.B. Ges. Naturf. Fr. Berlin, 63–74.

Bei-Bienko, *see* **Bienko, Bei-.**

Beklemishev, V. N. (1923). ["Sur quelques espèces de biocoenoses du lac Aral."] Bull. Inst. Rech. Biol. Perm, 1: 141–8. *Rf.*

Beklemishev, V. N. (1928). ["Structure and ecology of terrestrial communities."] Proc. Russ. Congr. Zool. 3: 26–7. *R.*

Beklemishev, V. N. (1928). ["Der Organismus und die Biocoenose: zum Problem der Individualität in der Biocoenologie."] Trav. Inst. Rech. Biol. Perm, 1: 127–49. *Rg.*

***Beklemishev, V. N. (1931).** ["Über die Anwendung einiger Grundbegriffe der Biocönologie auf tierische Komponente der Festlandbiocönosen."] Bull. Pl. Prot., Leningr. Ser. 1, 1: 278–358. *Rg.*

Beklemishev, V. N. (1934). ["Die täglichen Migrationen der Wirbellosen einem Komplex von Festlandbiocönosen."] Trav. Inst. Rech. Biol. Perm, 6: 119–208. *Rg.*

Beklemishev, V. N. & Igoshina, K. (1928). ["Untersuchungen über die Verteilung von Individuen verschiedener Ordnung in den Assoziationsflecken Filipenduletum hexapetalae und Deschampsietum."] Trav. Inst. Rech. Biol. Perm, 1: 171–82. *Rg.*

Berezhkov, R. P. (1927). ["A preliminary review of the injurious Acrididae of Western Siberia."] Bull. Plant Prot. Siberia, 2 (5): 40–52. *R.*

Berezina, V. M. (1937). ["Die Veränderung der Entomofauna des Bodens beim Uebergang aus Steppen-Verhältnisse in Waldverhältnisse."] Rev. Ent. U.R.S.S. 27: 77–112. *Rg.*

Berezina, V. M. & Stark, V. N. (1936). ["Areal distribution of the eastern May beetle (*Melolontha hippocastani* F.) in U.S.S.R."] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 28–32. *R.*

***Berg, L. S. (1922).** ["Climate and life."] Moscow. *R.*

***Berg, L. S. (1928).** ["Ten years' work (1917–1927) of the Bureau of Applied Ichthyology."] Bull. Bur. Appl. Ichth. U.S.S.R. 8: 183–99. *R.*

***Berg, L. S. (1930).** ["The landscape zones of the U.S.S.R."] Leningrad. *R.*

Berg, L. S. (1937). ["Progress in ichthyology during the period 1917–1937."] Bull. Acad. Sci. U.S.S.R. (Ser. Biol.), 1493–502. *Re.*

Berg, M. M. Ivanova- (1927). ["Guide to the literature of the animal world of Turkestan: animal world, agricultural pests, fishing, hunting and stock-raising."] Acad. Sci. U.S.S.R., Commission for the Investigation of Natural Resources in the U.S.S.R. Leningrad. 235 pp. *R.*

Bienko, G. Ya. Bei- (1928). ["A note on *Dociostaurus crucigerus brevicollis* Ev. (Acrididae) in W. Siberia."] Bull. W. Sib. Mus. 1: (8 pp.). *R.*

Bienko, G. Ya. Bei- (1930). ["The zonal and ecological distribution of Acrididae in the West Siberian and Zaisan plains."] Bull. Pl. Prot., Leningr. Ser 1, 1: 51–90. *R.*

Bienko, G. Ya. Bei- (1932). ["Manual for the locust record service."] Leningr. Ass. Contr. Pests Agric. For. U.S.S.R. Leningrad. 195 pp. *R.*

Bienko, G. Ya. Bei- (1936). ["Distribution and zones of injury of the Moroccan locust (*Dociostaurus moroccanus* Thnb.) in U.S.S.R."] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 16–20. *R.*

Bienko, G. Ya. Bei- (1936). ["The structure and dynamics of biocenoses of virgin and newly-cultivated areas."] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 75–6. *R.* (English abstract in Rev. Appl. Ent. A, 25: 137–60.)

Bienko, G. Ya. Bei- and others (1936). ["Characteristic insects and soil fauna in biocenoses of the Orenburg steppe in the Saverovsk-Khalulovsk district."] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 78–82. *R.*

Bilanovskii, I. D. (1935). ["Biological methods of control of injurious insects."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 2: 213–57. *U.*

Birulya, N. B. (1936). ["Les lois écologiques de la distribution stationnaire du petit spermophile (*Citellus pygmaeus* Pall.)."] Miscellany Inst. Zool. Moscow St. Univ. 3: 117–45. *Rf.*

***Bobrinskii, N. A. (1927).** ["Zoogeography and evolution."] Moscow.

Bogdanovskaya-Gienéf, *see* **Gienéf, Bogdanovskaya-.**

Bogorov, V. G. (1927). ["Zur Methodik der Bearbeitung des Planktons."] Russ. Hydrobiol. Zh. 6: 193–8. *Rg*.

***Bogorov, V. G.** (1932). ["On the methods of studying the benthos."] Bull. Oceanogr. Inst. Moscow, (6): 1–8. *Re*.

***Bogorov, V. G.** (1934). ["On the plankton organism's biomass."] Bull. All-Un. Inst. Mar. Fish. Oceanogr. 1: 1–18. *Re*.

***Bogorov, V. G.** (1934). ["On the term 'biomass of a plankton organism'."] Bull. All-Un. Inst. Mar. Fish. Oceanogr. 2: 26–9. *R*.

Bogoslovskii, A. S. (1929). ["Oekologische Studien an Rotifera, I."] Bull. Sta. Biol. Bolchevo, 3: 7–25. *Rg*.

Boitzova, M. K. (1931). ["The animal population of the lower layers of the Pinetum cladinosum."] Sci. Rep. Perm. St. Univ. 4: 97–152. *Rg*.

Boldureva, N. V. (1926). ["Zur Untersuchung des Lebens der Wiesensümpfe des Oka-Ueberschwemmungsgebietes."] Arb. Biol. Oka Sta. (Murom), 4: 125–60. *Rg*.

***Borutzkii, E. V.** (1932). ["Zur Frage über die Technik der Bodenfaunauntersuchungen."] Arb. Limnol. Sta. Kossino, 15: 5–42. *Rg*.

***Borutzkii, E. V.** (1934). ["Zur Frage über die Technik der quantitativen Untersuchungen der Bodenfauna. III. Zur Methodik der Bearbeitung des Seebenthos. Ein Vergleich des Frisch-Roh-(Formelen) Gewichts."] Arb. Limnol. Sta. Kossino, 18: 109–32. *Rg*.

***Borutzkii, E. V.** (1935). ["Zur Frage der Technik der quantitativen Untersuchungen der Bodenfauna."] Arb. Limnol. Sta. Kossino, 19: 5–19, 105–25. *Rg*.

[**Botanical Institute of Academy of Sciences, U.S.S.R.**] (1938). ["Vegetation of the U.S.S.R. Vol. 1."] Moscow and Leningrad. 664 pp.

Brodskii, A. L. (1928). ["Contributions to the knowledge of the Turkestan soil fauna."] Proc. Russ. Congr. Zool. 3: 67–8. *R*.

Brodskii, A. L. (1928). ["Foraminifera (Polythalamia) in Grundwasser der Wüste Kara-Kum."] Acta Univ. Asiae Med. Ser. 8*a*, 5: 1–16. *Rg*.

Brodskii, K. (1935). ["Contribution to the knowledge of the invertebrate fauna of the mountain streams of Central Asia. I. The River Issyk."] Acta Univ. Asiae Med. Ser. 8*a*, 15: 1–112. *Re*.

Brodskii, A. & Belyaeva, K. (1935). ["Materials for the knowledge of the protistenfauna of the soils of Betpak-Dala."] Acta Univ. Asiae Med. Ser. 7*d*, 3: 1–48. *Re*.

***Brodskii, A. L. & Yankovskaya, A. I.** (1929). ["Materials on the knowledge of the soil fauna of Middle Asia. II. The soil protofauna in the Kara-Kum desert."] Acta Univ. Asiae Med. Ser. 12*a*, 5: 1–38. *Re*.

Brotzkaya, V. A. & Zenkevich, L. A. (1936). ["Biological productivity of sea waters."] Zool. Zh. 15: 13–25. *Re*.

***Buistritzkii, P. N.** (1933). ["Der Oekologie der Acridoidea der steinernen Schlucht in den Umgebungen von Kinel (neben Samara)."] Moscow and Samara: OTIZ. *Rg*.

Bukovskii, V. (1935). ["On the criticism of the basic problems and concepts of biocenology."] Probl. Ecol. Biocenol. [2]: 74–99. *Re*.

Bukovskii, V. (1936). ["Die Tierbevölkerung der Wirbellosen der krimschen Buchenwaldes."] Trans. of the State Reservations, Ser. 2 (1): 5–103. *Rg*.

Burakova, L. (1929). ["Quantitative Analyse der Fauna von *Brassica oleracea* zu Peterhof."] Trav. Soc. Nat. Leningr. 59: 83–94. *Rg*.

Butovich [Butovitsch] V. (1936). "Neuere russische forstentomologische Literatur. Sammelbericht für die Jahre 1930–1934." Z. Angew. Ent. 23: 485–529.

Buturlin, S. A. (1935). ["A complete guide to the birds of the U.S.S.R."] 2 vols. Moscow and Leningrad: KOIZ. *R*.

Charlemagne, *see* **Sharleman'**.

***Chernai, A.** (1853). ["Fauna of the Kharkov government and a study of their habitats."] *R*.

Chetuirkina, I. (1928). ["Distribution of the Lumbricidae in the soils of the Troitsk District, Ural Region."] Trav. Inst. Rech. Biol. Perm, 2: 433–69. *Re*.

Chetuirkina, I. (1936). ["Distribution and zones of injury of *Calliptamus italicus* in Kazakhstan."] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 20–2. *R*.

***Chugunov [Tchugunoff], I. L.** (1923). ["An attempt at a quantitative evaluation of the sea-bottom fauna in the North Caspian region and in the Volga Delta."] Trans. Lab. Ichth. Astrakhan, 5 (1). *Re*.

Danilchenko, P. G. (1936). "On the ecology of the spawning migrations of the salmon." C.R Acad. Sci. U.R.S.S. 2: 81–4. *E*.

Danilova, M. M. & Shukhardin, V. N. (1936). ["A classification of the meadows of the valley of the River Kama between Perm and Solikamsk."] Bull. Inst. Rech. Biol. Perm, 10: 453–65. *Re.*

Danini, E. V. (1933). ["On the ecology of the rodents of the Troitsk Reserve and its environs."] Bull. Inst. Rech. Biol. Perm, 8: 105–22, 375–418. *Re.*

Deineka, D. I. (1935). ["Fifteen years of the Peterhof Biological Institute...."] Trav. Inst. Sci. Peterhof, 15: 3–30. *R.*

Deksbakh [Decksbach], N. K. (1923). ["The study of biological types of lakes in Western Europe and the necessity of such study in Russia."] Proc. Russ. Congr. Zool. 1: 48–50. *R.*

Deksbakh, N. K. (1925). ["Der Boden der Seen zu Kossino, als Milieu und seine Bewohner."] Arb. Biol. Sta. Kossino, 3–48. *Rg.*

Deksbakh, N. K. (1928). ["Modern opinions on the biological types of lakes (Lundbeck's scheme)."] Proc. Russ. Congr. Zool. 3: 364–7. *R.*

***Deksbakh, N. K. (1931).** ["Studien an den Teichen der Kossino-Umgegend (bei Moskau) auf regional-limnologischer Grundlage."] Arb. Limnol. Sta. Kossino, 12: 7–121. *Rg.*

***Deksbakh, N. K. (1934).** ["Seen des Bassins der rechten Nebenflüsse der Kljasma, der Senjga, und Uschma-Flüsse. Regional-limnologische Skizze eines Waldgebietes."] Arb. Limnol. Sta. Kossino, 18: 41–68. *Rg.*

Dement'ev, G. P. (1937). ["Twenty years of ornithological work in the U.S.S.R. (1917–1937)."] Zool. Zh. 16: 889–901. *R.*

Dergunov, N. I. (1923). ["The method of census of birds and an experiment on its efficiency with woodpeckers (*Dendrocopus major* L.)."] Proc. Russ. Congr. Zool. 1: 21–2. *R.*

Deryugin, K. M. (1925). ["Twenty-five years at the Murman Biological Station."] Trav. Biol. Sta. Murman, 1: 1–4. *R.*

[Deryugin, K. M.] (1925). ["The Peterhof Scientific Research Institute during the five years of its organisation."] Trav. Inst. Sci. Peterhof, 1: 1–81. *R.* (Has articles on the various laboratories, and good bibliographies.)

Deryugin, K. M. (1925). ["Reliktensee Mogilnoje (Insel Kildin im Barents-Meere)."] Trav. Inst. Sci. Peterhof, 2: 1–111. *Rg.*

Deryugin, K. M. (1928). ["Hydrobiological investigations in the Japanese sea."] Proc. Russ. Congr. Zool. 3: 32–4. *R.*

Deryugin, K. M. (1928). ["The organization of the Pacific Scientific Fishery Research Station of the Far East."] Bull. Pacific Fish. Res. Sta. 1: 5–75. *Re.* (*Also in German in Rev. Hydrobiol. Hydrogr. 15 (1926).)

Deryugin, K. M. (1928). ["Uebersicht der Tätigkeit des Naturwissenschaftlichen Instituts zu Peterhof."] Trav. Inst. Sci. Peterhof, 5: 4–35. *Rg.* (A ten-year review, with good bibliography.)

[Deryugin, K. M.] (1930). ["Summary of the activities of the Peterhof Natural Science Institute during the 10 years of its existence."] Trav. Inst. Sci. Peterhof, 7: 181–245. *R.*

Deryugin, K. M. (1935). ["La problématique des travaux du Laboratoire de Zoologie des Vertébrés et d'Hydrobiologie de l'Institut Biologique au Péterhof pendant les 15 ans de son existence ainsi que les perspectives de son évolution subséquente."] Trav. Inst. Sci. Peterhof, 15: 57–68. *Rf.*

***Deryugin, K. M. (1936).** ["Progress in Soviet hydrobiology in the field of marine research."] Advances Modern Biol. 5: 9–26. *R.*

***Deryugin, K. M. and others (1937).** ["Investigations of the fauna of the Arctic Seas of the Soviet Union."] Leningrad. *Re.*

Dogel [Dogiel], V. A. (1924). ["Quantitative studies on terrestrial fauna. An attempt at quantitative analysis of the fauna of meadows."] Rev. Zool. Russe, 4 (1): 117–54. *Re.*

Dogel, V. A. & Efremov, G. V. (1926). ["Quantitative studies on terrestrial fauna: II. Quantitative investigations of the ground of fir-tree forests."] Trav. Soc. Nat. Leningr. 55: 97–110. *Rg.*

Dogel, V. A. & Petrushevskii, G. (1935). ["An ecological study of the parasites of the salmon."] Probl. Ecol. Biocenol. [2]: 137–69. *Re.*

Dokhman, G. I. (1936). ["Essai d'une classification écologico-génétique de la végétation de la forêt-steppe d'Ischim."] Bull. Soc. Nat. Moscou, Sect. Biol. 44: 190–202. *Rf.*

***Domrachev, P. L. and others (1934).** ["Ichthyological investigation of the sea and the composition of ichthyological maps. A collection of papers on methodology and instructions for scientific research."] Bull. Inst. Freshwater Fish., Leningr. 18–19: 1–381. *R.*

***Drobov, V. P. (1928).** ["Sandwüste 'Kara-Kum' neben der Station Repetek und ihre Vegetation."] Acta Univ. Asiae Med. Ser. 8*b*, 1: 1–28. *Rg.*

Dul'keit, G. D. (1929). ["Contribution to the knowledge of the biology of the sable and the economy of the seal islands, Great Shantar."] Bull. Pacif. Fish. Res. Sta. 3 (3): 1–120. *Re.*

Duplakov, S. N. (1925). ["On knowledge of the biocenoses of submerged objects."] Russ. Hydrobiol. Zh. 4: 42–9. *Rg.*

Durnovo, Z. P. and others (1936). ["Changes in the fauna of injurious rodents and insects in biocenoses in abandoned and recently virgin land in the podsol (burnt forest) zone (Kirovsk district.)"] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 88–90. *R.*

Durymanova-Savik, *see* **Savik, Durymanova-.**

Elenkin, A. A. (1921). ["La loi de l'équilibre mobile dans les symbioses et les associations des plantes."] Bull. Chief. Bot. Gard. U.S.S.R. 20: 75–121. *Rf.*

§**Elton, C. (1934).** "The ecology of animals." (Translated into Russian by **D. N. Kashkarov** from the English edition of 1933.) Leningrad and Moscow. 83 pp.

Eversmann, E. (1840). "Mitteilungen über einige neue und einige weniger gekannte Säugethiere Russlands." Bull. Soc. Nat. Moscou, 13: 3–57.

Falkenshtein, B. Yu. (1936). ["Distribution of ground squirrels and their importance in U.S.S.R."] Summ. Sci. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 40–3. *R.*

***Fedchenko [Fedtschenko], B. de (1912).** "La végétation de la Russe d'Asie." Proc. Int. Bot. Congr. 1912, 2: 51–8.

Filip'ev, I. N. (1924). ["Essai d'une définition exacte des termes principaux se rapportent à la distribution des animaux habitant le fond des eaux."] Russ. Hydrobiol. Zh. 3: 1–8. *Rf.*

***Filip'ev, I. N. (1929*a*).** "The locust question in Soviet Russia." 4th Int. Congr. Ent. Ithaca, 1928, 2: 803–12.

***Filip'ev, I. N. (1929*b*).** "Life zones in Russia and their injurious insects." 4th Int. Congr. Ent. Ithaca, 1928, 2: 813–20.

Filip'ev, I. N. (1929*c*). ["Some regularities in distribution and propagation of gregarious noxious insects."] Recent Attainments and Perspectives in Agronomy, St. Inst. Exp. Agron., Bur. Appl. Ent. 6–9: 1–24. *R.*

Formozov [Formosov], A. N. (1928). "Mammalia in the steppe biocenose." Ecology, 9: 449–60.

Formozov, A. N. (1933). ["Maps of the geographical distribution of economic mammals and birds. Problems and methods of mapping biological data."] Zool. Zh. 12: 110–16. *Rg.*

Formozov [Formosof], A. N. (1933). "The crop of cedar nuts, invasions into Europe of the Siberian nutcracker (*Nucifraga caryocatactes macrorhynchus* Brehm.) and fluctuations in numbers of the squirrel (*Sciurus vulgaris* L.)." J. Anim. Ecol. 2: 70–81. (Also in *Miscellany Inst. Zool. Moscow St. Univ. (1933). 1: 64–70. *R.*)

Formozov, A. N. (1934). ["On the problem of inter-specific competition. Mutual relations of the squirrel (*Sciurus vulgaris* L.), the crossbill (*Loxia curvirostra* L.) and the great spotted woodpecker (*Dryobates major* L.)."] C.R. Acad. Sci. U.R.S.S., Ser. 3: 197–201. *Re.*

Formozov, A. N. (1934). ["Birds of prey and rodents...."] Zool. Zh. 13: 664–700. *Re.*

Formozov, A. N. (1934). ["The Lake Region of the Forest-Steppe and Steppe of Western Siberia as a breeding area of water-fowl."] Bull. Soc. Nat. Moscou, Sect. Biol. 43: 256–86. *Re.*

Formozov, A. N. (1934). ["On the biology of the hazel grouse (*Tetrastes bonasia volgensis* But.) from observations in the Gorkovski (Nizhni-Novgorod) District."] Bull. Soc. Nat. Moscou, Sect. Biol. 43: 1–34. *Re.*

Formozov, A. N. (1935). ["Fluctuations in numbers of animals of economic importance."] Moscow and Leningrad: KOIZ. 108 pp. *R.*

Formozov, A. N. (1936). ["Migrations of the common squirrel (*Sciurus vulgaris*) in U.S.S.R."] Trav. Zool. Inst. Acad. Sci. U.R.S.S., Ser. 3: 97–164. *R.*

Formozov, A. N. (1937*a*). ["Materials on the ecology of aquatic birds according to observations made on the lakes of the state Naurzum Reserve (Northern part of Kazakhstan)."] M. A. Menzbir Memorial: 551–95. *Re.*

Formozov, A. N. (1937*b*). ["On the utilization of the fauna of terrestrial vertebrates and some problems of its reconstruction."] Zool. Zh. 16: 407–42. *Re.*

†**Formozov, A. N. (1937*c*).** ["A short summary of works on the ecology of birds and mammals during the 20 years 1917–1937."] Zool. Zh. 16: 916–49. *R.*

Formozov, A. N. & Birulya, N. B. (1937). ["Zur Frage der gegenseitigen Verhältnisse der Raubvögel und Nagetiere."] Wiss. Ber. Moskau St. Univ. 13: 72–84. *Rg.*

Formozov, A. N., Naumov, N. P. & Kiris, I. D. (1934). ["Ecology of the red squirrel."] Moscow and Leningrad. 128 pp. *Re.*

Formozov, A. N. & Prosvirnina, I. B. (1935). ["L'activité des rongeurs au Caucase et leur influence sur les phytocenoses des pâturages et des prairies."] Bull. Soc. Nat. Moscou, 44: 82–9. *Rf.*

Formozov, A. N. & Voronov, A. G. (1935). "Principal features of the activity of rodents on pastures and meadow land." C.R. Acad. Sci. U.R.S.S. 3: 370–2. *E.*

***Fortikov, I. P. (1936).** ["The biosphere."] Priroda, 9: 27–32. *R.*

***§Freidrichs, K. (1932).** ["Ecological principles of applied zoology and entomology."] (Russian translation of "Grundfragen und Gesetzmässigkeiten der land- und forstwirtschaftlichen Zoologie insbesondere Entomologie.") Moscow.

***Fridolin, V. Yu (1935).** ["The life of mountain tundras."] Expeditions of the Acad. Sci. U.S.S.R. 1934: 67–75. *R.*

Fridolin, V. Yu. (1936). ["Animal-plant communities of the mountain country of Khibin: Biocenotic Investigations 1930–1935."] I. Moscow-Leningrad: Acad. Sci. 295 pp. *R.*

Fridolin, V. Yu. (1936). "[Kukis-Vum-Chorr], le plateau central des Monts Khibines au point de vue biocénotique." Rev. Ent. U.R.S.S. 26: 165-82. *Fr.*

Fridolin, V. Yu. (1936). ["Biocoenological and ecological research work and museum on the [K]Hibin Mountain Station of the Academy of Sciences (1930–1934) of U.S.S.R."] Probl. Ecol. Biocenol. 3: 296–304. *Re.*

§Gates, R. Ruggles (1928). "Notes on the tundra of Russian Lapland." J. Ecol. 16: 150–60.

Gause = Gauze.

Gause, G. F. (1930). "Studies on the ecology of the Orthoptera." Ecology, 11: 307-25.

Gause, G. F. (1931). "The influence of ecological factors on the size of population." Amer. Nat. 45: 70–6.

Gause, G. F. (1932). "Experimental studies on the struggle for existence, I. Mixed population of two species of yeast." J. Exp. Biol. 9: 389–402.

Gause, G. F. (1932). "Ecology of populations." Quart. Rev. Biol. 7: 27–46.

Gauze, G. F. (1933). ["Mathematical methods applied to the problem of the struggle for existence."] Zool. Zh. 12 (3): 170–7. *R.*

Gause, G. F. (1934). "Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence." Science, 79: 16–17.

Gause, G. F. (1934). "Über die Konkurrenz zwischen zwei Arten." Zool. Anz. 105: 219–22.

Gause, G. F. (1934). "Über einige quantitative Beziehungen in der Insekten-Epidemiologie." Z. Angew. Ent. 20: 619–23.

Gauze, G. F. (1934). ["Problems of natural selection."] Advances Modern Biol. 3 (4): 480–90. *R.*

Gause, G. F. (1934). ["The mathematical theory of the struggle for existence and its application to populations of yeast cells."] Bull. Soc. Nat. Moscou, Sect. Biol. 43: 63–87. *Re.*

Gause, G. F. (1934). "The struggle for existence." Baltimore. 163 pp.

Gause, G. F. (1934). "Untersuchungen über den Kampf ums Dasein bei Protisten." Biol. Zbl. 54: 536–47.

Gause, G. F. (1935). "Experimentelle Untersuchungen über die Konkurrenz zwischen *Paramecium caudatum* und *Paramecium aurelia*." Arch. Protistenk. 84: 207–24.

Gause, G. F. (1935). "Experimental demonstration of Volterra's periodic oscillations in the numbers of animals." J. Exp. Biol. 12: 44–8.

Gauze, G. F. (1935). ["Studies on the struggle for existence in mixed populations."] Zool. Zh. 14: 243–69. *R(e).*

Gauze, G. F. (1935). ["Laws governing the mass increase of injurious insects (a review of the literature)...."] Zool. Zh. 14: 413–38. *R.*

Gause, G. F. (1935). "Vérifications expérimentales de la théorie mathématique de la lutte pour la vie." Actualités Sci. Industr. 277: 1–63. Paris.

Gauze, G. F. (1936). ["On certain basic problems in biocoenology."] Zool. Zh. 15: 363–81. *Re.*

Gause, G. F. (1937). "Experimental populations of microscopic organisms." Ecology, 18: 173–9.

Gause, G. F. (1937). "The principles of biocoenology." Quart. Rev. Biol. 11: 320–36.

Gause, G. F. & Alpatov, V. V. [W. W.] (1931). "Die logistische Kurve von Verhulst-Pearl und ihre Anwandung im Gebiet der quantitativen Biologie." Biol. Zbl. 51: 1–14.

Gause, G. F., Nastukova, O. K. & Alpatov, V. V. [W. W.] (1934). "The influence of biologically conditioned media on the growth of a mixed population of *Paramecium caudatum* and *P. aurelia*." J. Anim. Ecol. 3: 222–30.

Gause, G. F., Smaragdova, N. P. & Vitt [Witt], A. A. (1936). "Further studies of interaction between predators and prey." J. Anim. Ecol. 5: 1–18.

†**Gauze, G. F. & Vitt, A. (1934).** ["On the periodic fluctuation in the numbers of animals: a mathematical theory of the relaxation interaction between predators and prey and its application to a population of Protozoa."] Bull. Acad. Sci. U.R.S.S. 1551–9. *Re.*

Gause, G. F. & Witt [Vitt], A. A. (1935). "Behavior of mixed populations and the problem of natural selection." Amer. Nat. 69: 596–609.

***Gel'man, Ya. M. (1924).** ["Hydrobiology."] Leningrad. *R.*

***Geptner [Heptner], V. G. (1934).** "Russische Literatur im Jahre 1933." Z. Säugetierk. 9: 35–46.

Geptner, V. G. (1936). ["General zoogeography."] Moscow and Leningrad. 548 pp. *R.*

Gienéf, I. D. Bogdanovskaya- (1928). ["Die natürlichen Rayons [Regions] des nord-westlichen Teiles des Leningrader Gebietes."] Trav. Inst. Sci. Peterhof, 5: 103–18 (with map). *Rg.*

Gienéf, I. D. Bogdanovskaya- (1928). ["Die Vegetation der Hochmoore des russischen Ostbaltikums."] Trav. Inst. Sci. Peterhof, 5: 265–377. *Rg.*

Gilyarov [Gilarov], M. S. (1937). "The fauna of injurious insects of arable land." Bull. Ent. Res. 28: 633–7.

Gladkov, N. A. (1934). ["The distribution of ornithological stations on a lake in the plains."] C.R. Acad. Sci. U.R.S.S. 2: 60–4. *Re.*

Gladkov, N. A. (1936). ["The ecological peculiarities of the River Amu-Sarja 'Pojma' [flood-plain] as regards its ornithofauna."] Probl. Ecol. Biocenol. 3: 253–65. *Re.*

Glumov, G. A. (1936). ["An attempt at applying the method of linear transects to the study of a real and projective cover of some steppe phytocoenoses."] Bull. Inst. Rech. Biol. Perm, 10: 353–62. *Re.*

Gorbunov, G. [P.] (1934). ["Biological indicators and their importance in the study of the Arctic [zooplankton]."] Arctica, Leningr. 2: 113–25. *Re.*

Gorbunov, G. P. (1937). ["Hydrobiological researches in the northern seas of U.S.S.R. during 20 years."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1527–35. *Re.*

Grese, B. S. (1929). ["Zur Biologie periodischer Kleingewässer."] Russ. Hydrobiol. Zh. 8: 38–49. *Rg.*

Grigoreva, T. G. (1938). ["On methods of estimating the soil fauna."] Plant Protection, Leningr. (17): 97–110. *Re.*

Grivanov, K. P. (1936). ["Geographical distribution and zones of economic importance of the slug (*Agriolimax*) in European Russia."] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 34–7. *R.*

Gudoshchikova, V. (1928). ["The diurnal migrations of the insects in a complex of plant associations."] Trav. Inst. Rech. Biol. Perm, 1: 299–328. *Re.*

Gur'yanova, E. L. (1923). ["The biocenosis of rhizoids of *Laminaria* in the Barents Sea."] Proc. Russ. Congr. Zool. 1: 47–8. *R.*

Gur'yanova, E., Zaks, I. & Ushakov, P. (1925). ["Vergleichsübersicht des Littoral der russischen Nördlichen Meere."] Trav. Sta. Biol. Murman, 1: 110–30, 190. *Rg.*

Heptner, *see* **Geptner.**

Idelson, M. S. (1934). ["Materials for the quantitative evaluation of the bottom fauna of the Barents, White and Kara Seas, 7. Distribution of the benthos biomass in the southern Barents Sea. The influence of different factors on the density of sea bottom population."] Trans. Oceanogr. Inst. Moscow, 3 (4): 49–74. *Re.*

Igoshina, K. N. (1928). ["Pflanzengesellschaften auf dem Alluvium der Flüsse Kama und Tschussowaja."] Trav. Inst. Rech. Biol. Perm, 1 (2–3): 150–70. *Rg.*

Il'enko, M. I. (1935). ["On the problem of habitat distribution of the egg pods of grasshoppers."] Bull. Pl. Prot. Siberia, 2 (4): 45–57. *R.*

Il'inskii, A. M. (1931). ["A new method of quantitative statistical analysis of red spider infestation (*Epitetranychus althacae* v.H.)."] Plant Protection, Leningr. 8: 299–301. *Re.*

Il'un, B. S. (1927). ["Biocenoses of the sea of Azov."] Proc. Russ. Congr. Zool. 2: 276–7. *R.*

***Ioganzen, B. G. (1935).** ["A brief review of the scientific research work of the W. Siberian section of the All-Union Institute of Marine Fisheries and Oceanography in 1931–35."] Trans. W. Siberian Sect., All-Un. Inst. Mar. Fish. Oceanogr. 2: 1–17. *R.*

Isakov, V. F. (1936). ["Taiga vegetation as food resource for the squirrel."] Probl. Ecol. Biocenol. 3: 293–5. *Re.*

***Ivanenko, I. D. (1936).** ["Contribution to the knowledge of the biocenoses of preserved steppe in Askanya Nova."] Trans. Kharkov. Zoobiol. Inst. 1: 217–29. *U.*

Ivanov, E. N. (1934). ["On the biology and ecology of *Oedallus decorus* Germ."] Acrididae of Central Asia, Central Asiatic Inst. Plant Prot. Tashkent: 113–23. *R.*

Ivanov, E. N. (1934). [The biology and ecology of *Ramburiella turcomana* F.W.] Acrididae of Central Asia, Central Asiatic Inst. Plant Prot. Tashkent: 124–49. *R.*

Ivanov, S. P. & Zhitkevich, O. N. (1937). ["A survey of the outbreaks of *Loxostege sticticalis* in the main sugar-beet zone (Forest-steppe of the Ukr. S.S.R., Kursk and Voronezh regions, R.S.F.S.R.) and in the adjoining steppe regions of the Ukr. S.S.R. in 1935."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 4: 111–68. *Ure.*

Ivlev, V. S. (1931). "Zum Studium der Biologie des Flussbrandes des Flusses Ob." Zool. Anz. 96: 23–30.

Ivlev, V. S. (1933). "Ein Versuch zur experimentellen Erforschung der Ökologie der Wasser-biocönosen." Arch. Hydrobiol. Plankt. 25: 177–91.

Izotov, I. P. (1932). ["Investigations on the interrelations between *Tyto alba guttata* Brhm., and small rodents."] Kiev: Ukr. Acad. Sci., Dept. Nat. Sci. and Technique, 93–100. *U.*

Jurgenson, *see* **Yurgenson.**

Kachaeva, Z. F. & Rubtzov, I. A. (1935). ["A geobotanical study of the locust reservation in the Balagansk steppe."] Bull. Pl. Prot. Siberia, 2: 278–88. *R.*

Kadzevitch, I. S. (1935). ["Biological observations on *Chorthippus albomarginatus* De Geer in Kuznetzk steppe."] Bull. W. Sib. Pl. Prot. Sta. 1 (9): 119–36. *Re.*

†**Kalabukhov, N. I. (1933).** ["The duration of life of *Citellus pygmaeus* Pall. (Rodentia) studied by means of the banding method.]" Wiss. Ber. Moskau St. Univ. 1: 1–6. *Re.*

†**Kalabukhov, N. I. (1935).** ["On the causes of fluctuations in numbers of mouse-like rodents."] Zool. Zh. 14: 209–42. *Re.*

†**Kalabukhov, N. I. (1937).** ["Principal laws of the dynamics of mammal and bird populations."] Advances Modern Biol. 7: 505–31. *R.*

†**Kalabukhov, N. I. (1937).** ["Results of 20 years' (1917–1937) investigations of the ecology of injurious rodents of the U.S.S.R."] Zool. Zh. 16: 950–71. *R.*

†**Kalabukhov, N. I. & Raevskii, V. V. (1933).** ["Methods for the study of certain problems in the ecology of mouse-like rodents."] Rev. Microbiol., Saratov, 12: 47–62. *Rg.*

†**Kalabukhov, N. I. & Raevskii, V. V. (1935).** ["A study of migrations in ground squirrels (*Citellus pygmaeus* Pall.) in the steppe part of the Northern Caucasus by means of the banding method."] Probl. Ecol. Biocenol. [2]: 170–95. *Re.*

Kalashnikov, L. N. (1934). ["Versuch einer graphischen Darstellung des Vegetationwechsels im Raum."] Bot. Zh. 19: 26–32. *Rg.*

Kallinikova, T. N. (1927). ["Results of quantitative investigations of the fauna of fruit trees."] Trav. Soc. Nat. Leningr. 57 (2): 3–34. *Rg.*

Kallinikova, T. N. (1932). ["Quantitative Untersuchung der Fauna der Landbäume des Krimgebirges."] Trav. Soc. Nat. Leningr. 61: 30–70. *Rg.*

***Karzinkin, G. S. (1925).** ["Versuch einer praktischer Lösung der Biocoenosenfrage."] Arb. Hydrobiol. Sta. am See "Glubokoje", 6: 36–45. *Rg.*

Karsinkin, G. S. (1926–7). ["Versuch einer praktischen Begründung des Begriffs 'Biocönose'."] Rev. Zool. Russe, 6 (4): 97–133; 7 (1): 3–33; 7 (2): 34–76; 7 (3): 4–14. *Rg.* (4th part entirely German summary.)

Karzinkin, G. S. (1927). ["An attempt at a practical statement of the concept 'Biocenosis'."] Proc. Russ. Congr. Zool. 2: 279–81 *R.*

Karzinkin, G. S. (1936). ["Theorie der biologischen Produktivität des Gewässer als Arbeitsmethode."] Zool. Zh. 15: 245–51. *Rg.*

***Karzinkin, G. S. & Kuznetzov, S. I. (1931).** ["New methods in limnology."] Arb. Limnol. Sta. Kossino, 13/14: 47–68. *Rg.*

***Kashkarov, D. N. (1927).** ["The quantitative method in the field study of vertebrates and analysis of the data obtained."] Acta Univ. Asiae Med. Ser. 8*a*, 1: 1–24. *Re.*

Kashkarov, D. N. (1928). ["Ecology in modern zoology."] Proc. Russ. Congr. Zool. 3: 35–7. *R.*

Kashkarov, D. N. (1928). ["The fundamental types of communities of vertebrates in central Asia."] Proc. Russ. Congr. Zool. 3: 72–3. *R.*

Kashkarov, D. N. (1928). ["Methods of collecting data for vertebrates and the analysis of the data obtained."] Proc. Russ. Congr. Zool. 3: 70–1. *R.*

***Kashkarov, D. N. (1928).** ["An ecological study of the lake district of Biili-Kul, Ak-Kul and Ashchi-Kul."] Acta Univ. Asiae Med. Ser. 8*a*, 2: 1–54. *Re.*

Kashkarov, D. N. (**1931**). ["Ecology in modern zoology."] J. Ecol. and Biocenol. 1: 111–32. *Re.*

***Kashkarov, D. N.** (**1933**). ["Environment and community (Principles of synecology); a course given at the Middle Asiatic State University, Tashkent."] Moscow. *R.*

Kashkarov, D. N. (**1934**). ["An ecological survey of the vertebrate fauna in Arslanbob, North Ferghana."] Probl. Ecol. Biocenol. [1]: 56–114.

***Kashkarov, D. N.** (**1934**). ["The contents and direction of ecology"; in the symposium: "Basic aims and direction of growth of Soviet ecology."] Sov. Bot. (3): 1–68 (especially pp. 10–18 and 63–6). *R.*

Kashkarov, D. N. (**1934**). [In the symposium "What is a phytocenosis?"] Sov. Bot. (5): 21–4.

Kashkarov, D. N. (**1935**). ["A zoo-ecological sketch of the Eastern part of the Betpak-Dala desert."] Acta Univ. Asiae Med. Ser. 8*a*, 20: 1–30. *Re.*

Kashkarov, D. N. (**1937*a***). ["The ecology of domestic animals as shown in the Karakul sheep."] Priroda: 47–67. *R.*

Kashkarov, D. N. (**1937*b***). ["Soviet zoo-ecology, its status, progress in 20 years, and a perspective of its growth."] Priroda: 212–29. *R.*

Kashkarov, D. N. (**1937*c***). ["The ecology of domestic animals: its scope, tasks and methods."] M.A. Menzbir Memorial: 149–73. *Re.*

Kashkarov, D. N. (**1938**). ["Principles of the ecology of animals."] Moscow and Leningrad: MEDGIZ. 601 pp. *R.* (Reviewed in J. Anim. Ecol. (1939) 8: 171–2.)

Kashkarov, D. [N.] & Korovin, E. [P.] (**1931**). ["Essay on the analysis of the ecological routes of the distribution of the flora and fauna in Middle Asia."] J. Ecol. Biocenol. 1: 28–87. *Re.*

***Kashkarov, D. N. & Korovin, E. P.** (**1934**). ["Ecology as a means of Socialistic economy."] Acta Univ. Asiae Med. Ser. 8*c*, 1: 1–35. *Re.*

***Kashkarov, D. N. & Korovin, E. P.** (**1937**). ["Life of deserts."] Moscow and Leningrad: BIOMEDGIZ. *R.* (Reviewed by V. V. Alpatov in Zool. Zh. (1937), 16: 190–1. *R.*)

Kashkarov, D. N. & Kurbatov, V. P. (**1929**). ["Preliminary ecological survey of the vertebrate fauna of the Central Kara-Kum Desert in West Turkestan."] Ecology, 11: 35–60. (*Also in Acta Univ. Asiae Med. (1929) Ser. 12*a*, 7: 1–68. *Re.*)

***Kashkarov, D. N. & Stanchinskii, V. V.** (**1935**). ["A course in the zoology of vertebrate animals."] Moscow and Leningrad: BIOMEDGIZ. *R.*

Kashkarov, D. [N.], Zhukov, A. & Stanyukovich, K. (**1937**). ["The cold desert of Central Tian-Shan: the results of the expedition of the Leningrad State University in the summer of 1934 "] Leningrad. 167 pp. *Re.*

Katz, N. Ya. [**J.**] (**1926**). "Sphagnum bogs of central Russia: phytosociology, ecology and succession." J. Ecol. 14: 177–202.

Katz, N. Ya. (**1930**). ["Les principes des associations des plantes et la conception de l'association."] Bull. Soc. Nat. Moscou, Sect. Biol. 39: 147–76. *Rf.*

Katz, N. Ya. (**1934**). ["Über die Grundprobleme und die neue Richtung der gegenwärtigen Phytocönologie."] Bull. Soc. Nat. Moscou, Sect. Biol. 43: 188–221. *Rg.*

***Kavetzkii, R. E.** (**1936**). ["The Institute of Experimental Biology and Pathology in Kiev."] Priroda, 8: 128–30. *R.*

***Keller, B.** (**1914**). ["In Berg und Thal des Altai. I."] Kazan. *Rg.*

Keller, B. A. (**1927**). "Distribution of vegetation on the plains of European Russia." J. Ecol. 15: 189–309.

***Keller, B. A.** (**1927**). ["Russian progress in geobotany as based upon the study of soils."] Acad. Sci. U.S.S.R. Russ. Pedolog. Inst. (13): 1–34. *Re.*

Kharitonov, D. E. (**1931**). ["Die von M. K. Boizowa [Boitzova] in den unteren Schichten des Pinetum Cladinosum in Kurja bei Perm gesammelten Spinnen."] Trav. Inst. Rech. Biol. Perm, 4: 153–61. *Rg.*

***Kirichenko, A. N.** (**1926**). ["A study of the ecology and biology of *Calliptamus italicus* L. [locust] in the steppe zone of Ukraine."] Odessa Reg. Agric. Exp. Sta. Ent. Dep. (1): 47 pp. *R.* (English abstract in Rev. Appl. Ent. A, 15: 12.)

Kirichenko, A. N. (**1936**). ["The distribution of scale insects (Homoptera, Coccidae) in U.S.S.R. from the zoogeographical and ecological points of view."] Plant Protection, Leningr. (9): 68–75. *R.*

Kirikov, S. V. (**1936**). ["Über die ökologischen Zusammenhänge zwischen Nussknacker (*Nucifraga caryocatactes* L.) und Tanne (*Picea*)...."] Bull. Acad. Sci. U.R.S.S. Ser 3, 1936: 1235–50. *Rg.*

Kirshenblat, Ya. D. (**1936**). ["Fauna der Nester der Säugetiere und Vögel."] Probl. Ecol. Biocenol. 3: 47–60. *Rg.*

Kirshenblat, Ya. D. (1938). ["The laws of the dynamics of the parasite faunas of mouse-like rodents."] Leningrad State University. 92 pp. *R.*

Kir'yanova, E. S. (1936). ["Zur Frage über die vertikale und horizontale Verteilung der Fauna der Wirbellosen in den Erdschichten der Umgegend von Tashkent."] Trav. Inst. Zool. Acad. Sci. U.R.S.S. Ser 3: 309–52. *Rg.*

Kistyakovskii, A. B. (1932). ["Birds in the [fruit] gardens of the lower reaches of the Kuban."] Bull. Pl. Prot., Leningr. Ser. 4, 2: 111–40. *Re.*

Klyuge, G. (1936). ["The biological work of the polar station at Cape Zhelaniya in the years 1934–5."] Bull. Arctic Inst. U.S.S.R. 4: 170–2. *R.*

Knipovich, N. M. (1937). ["Hydrobiological studies of the Caspian sea."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.) (3): 1555–69. *Re.*

***§Kobelt, V. (1903).** ["Geographic distribution of animals in cold and temperate zones of the northern hemisphere."] (Translated into Russian from the German edition of "Die Verbreitung der Tierwelt", 1902.) St. Petersburg.

Kolesov, V. G. (1930). ["Oekologie der Eintagsfliegenlarven (Ephemeridenlarven)."] Bull. Sta. Biol. Bolchevo, 4: 130–51. *Rg.*

Kol'tzov, N. K. (1937). ["Progress in Soviet science in the field of biology in two decades."] Biol. Zh. 6: 929–46. *R.*

Konakov, V. & Onissimova [Z.] (1931). ["Ein Versuch der bei einer Excursion gewonnenen Characteristik der Stationen der südlichen Hälfte des Bogutscharer Kreises vom Gouvernement Woronesch der U.S.S.R."] Ber. Ges. Wiss. Arb. Erforsch. Nat. Erzeugungskräfte Zen. Tschernosjem Geb. Voronezh. 1 (2): 60 pp. *Rg.*

Konakov [Konakow], N. & Onissimova, Z. (1931). "Ein einfaches Biocönometer zur Auszählung der Insektenfauna der Grasdecke." Z. Angew. Ent. 18: 189–91.

***Korovin, E. P. (1936).** ["Scientific work of the Biological Institute of the Middle Asiatic State University at Tashkent."] Socialist. Sci. and Tech. 1: 92–4. *R.* ♯

Korovin, E. P. & Kashkarov, D. N. (1933). ["The desert types of Turkestan."] Acta Inst. Bot. Acad. Sci. U.R.S.S. Ser. 3, 1: 301–31. *Re.*

Korsakov, M. N. Rimskii- (1935). ["Forest entomology."] Leningrad. 482 pp. *R.*

***Koshko, K. & Lisitzuin, P. (1937).** ["On the influence of food crop on the dynamics of the squirrel population."] Zool. Zh. 16: 130–4. *Re.*

Kosobutzkii, M. I. (1936). ["On the methods of quantitative census in the ecological study of insect pests, diseases and weeds in cotton fields."] Probl. Ecol. Biocenol. 3: 79–139. *Re.*

Kotovshchikova, M. A. (1936). ["Examination of practical methods used at observation posts for the estimation of rodents."] Summ. Sci. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 540–2. *R.*

Kozhanchikov, I. V. (1936). ["The role of ecological factors in the distribution of *Pieris brassicae*."] Plant Protection, Leningr. (11): 40–57. *Re.*

***Kozhanchikov, I. V. (1936).** ["On the periodicity of mass propagation of insect pests."] Bull. Pl. Prot. Leningr. Ser. 1, 19: 1–35. *Re.*

Kozhevnikov, A. V. (1936). ["Matériaux sur la dynamique des stratification de l'herbage des prairies."] Bull. Soc. Nat. Moscou, Sect. Biol. 44: 203–12. *Rf.*

Kozhevnikov, A. V. (1937). ["Through tundra, forest, steppe, and desert; sketches of plant life in U.S.S.R."] Moscow and Leningrad: BIOMEDGIZ. 232 pp. *R.*

Krasovskii, P. N. and others (1934). ["The vegetation of some river valleys in the West Cis-Ural region."] Bull. Inst. Rech. Biol. Perm, 9: 15–35. *Re.*

Kruger, V. A. & Luton, A. A. (1936). ["Geobotanical and soil studies in the valley of the River Kama and its tributaries with the construction of the Levshino dam."] Bull. Inst. Rech. Biol. Perm, 10: 417–53. *Re.*

Kulagin, N. M. (1928). ["Works on applied zoology of the Moscow section of the Commission of Natural Resources of U.S.S.R. (KEPS)."] Proc. Russ. Congr. Zool. 3: 397. *R.*

Kulagin, N. M. (1936). ["On the work of the Laboratory of Entomology in 1933."] Miscellany Inst. Zool. Moscow St. Univ. 3: 188–9. *Re.*

Kulagin, N. M. (1937). ["A sketch of the most important works on entomology during the last 20 years."] Zool. Zh. 16: 871–88. *R.*

Kul'tiasov, M. V. (1931). ["Plant associations, communities and formations."] J. Ecol. Biocenol. 1: 138–45. *R.*

Kuznetzov [Kusnezov], N. I. (1893, 1897, 1898, 1899 and 1904). "Über der über Russland erschienenen phytogeographischen Arbeiten." Engler's Bot. Jb., Literaturberichte, 15: 64–94; 22: 24–44; 24: 58–80; 26: 16–42; and 29: 5–21.

***Kuznetzov, S. I. (1934).** ["Microbiological investigations in the study of the oxygenous regime of lakes."] Microbiologia, U.S.S.R. 3: 486–505. *Re.*

Kuznetzov, B. A. (**1935**). ["Über einige Gesetzmässigkeiten der Säugetierverbreitung im europäischen Teil des U.d.S.S.R."] Zool. Zh. 15: 96–127. *R.*

Kuznetzov, B. A. (**1937**). ["On a certain regularity in the distribution of mammals over the European part of the U.S.S.R."] Zool. Zh. 16: 165–82. *Re.*

Kuzyakin, A. P. (**1936**). ["The conditions of animals inhabiting the hollows of trees."] Probl. Ecol. Biocenol. 3: 266–74. *Re.*

***Lastochkin, D. A.** (**1927**). "Biosoziologische Studien in der Litoralregion einiger russischer Seen." Verh. Int. Vereinig. Limnol. Stuttgart, 3: 262–7.

Lastochkin, D. A. (**1931**). "Beiträge zur Seetypenlehre." Arch. Hydrobiol. Plankt. 22: 546–79.

Lastochkin, D. A. (**1937**). ["Hydrobiological science connected with studies of the benthos of lakes and their classification."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1571–81. *Re.*

Laptev, M. K. (**1935**). ["On the methods of census of rodents."] Trans. Turkmen. Agric. Inst. 1: 109–49. *Re.*

***Lavrenko, E. M.** (**1928**). ["Types of steppes in the Ukraine."] Priroda, 1928: 746–50. *R.*

Lavrenko, E. M. (**1931**). "The general characteristics of the Ukrainian vegetation." Contr. Ukr. Soil. Res. 3: 11–37. (As cited in Biol. Abstr. 9: 15417.)

Lavrov, N. P. (**1935**). ["On the biology of the common polecat."] Bull. Soc. Nat. Moscou, Sect. Biol. 24: 362–73. *Rf.*

***Lebedev, A. G.** (**1933**). ["Über die gesetzmässige Beziehung zwischen Bienen und Pflanzen."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 1: 5–13. *Ug.*

***Lebedev, A. G.** (**1933**). ["Zur Kenntnis der Fauna und Oekologie der blütenbeständen den Insekten."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 1: 51–78. *Ug.*

Lebedev, A. G. (**1935**). ["Materials for the study of biocenoses in foliate forests. II."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 2: 19–55. *Ure.*

***Lebedev, A. G.** (**1936**). ["Materials for the study of biocenoses in foliate forests. III."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 3: 25–71. *U.*

Lebedev, A. G. & Savenkov, A. N. (**1931**). ["Contributions to the study of the biocenosis of the pine forest."] Plant Protection, Leningr. 7: 1–17. *R.*

Lepeshkin, S. N., Zimin, L. S., Ivanov, E. N. & Zakhvatkin (**1934**). ["Locusts of Middle Asia."] All-Union Acad. Agric. Sci., Middle-Asiat. Inst. Plant. Prot. Moscow and Tashkent: SAOGIZ. 244 pp. *R.*

Leskov, A. I. (**1936**). ["Geobotanische Skizze der Strandwiesen an der Malosemelshaja Küste des Barents-Meeres."] Bot. Zh. 21: 96–116. *Rg.*

***Levitt, M. M.** (**1935**). ["Ueber einige allgemeine Fragen der Oekologie."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 1: 79–95. *Ug.*

Levitt, M. M. & Ivanov, S. P. (**1935**). ["On the fecundity in insects as related to some objects of ecology and practical entomology."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 2: 171–91. *Ure.*

Lignau, N. G. (**1928**). ["Contributions to the methods of a quantitative exploration of the terrestrial fauna."] Proc. Russ. Congr. Zool. 3: 77–8. *R.*

Lindgolm, V. A. (**1936**). "Eine neue Helicella (Helicidae, Gastropoda) aus der Krim, nebst Notizen zu Oekologie einiger Landschnecken." Trav. Zool. Inst. Acad. Sci. U.R.S.S. Ser. 3: 439–42. *G.*

Lipin, A. N. (**1925**). ["Über die quantitative Methodik bei der Berechnung von Bodenorganismen."] Russ. Hydrobiol. Zh. 4: 50–3. *R.*

Livanov, N. A. (**1923**). ["A system of sea biocenoses."] Proc. Russ. Congr. Zool. 1: 60–1. *R.*

Livanov, N. A. (**1927**). ["The system of biocenoses of the sea benthos."] Proc. Russ. Congr. Zool. 2: 287–8. *R.*

Lomakina, N. B. (**1936**). ["Development and improvement in estimation of numbers of mouse-like rodents in hot-houses, stacks and premises."] Summ. Sci. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 542–5. *R.*

Makaryan, M. Ya. (**1934**). ["Contributions to the knowledge of Orthopterous fauna of Abaran (Armenia)."] Bull. Inst. Sci. R.S.S. Armenie, Erivan, 1: 77–86. *Armenian and Re.*

***Markun, M. I.** (**1936**). ["The Kama Biological Station."] Priroda, 9: 125–7. *R.*

Meklenburtzev, R. N. (**1935**). ["Zur Ökologie und Verbreitung einiger Nagetiere im ebene-Teil des Zerawschantales."] Acta Univ. Asiae Med. Ser. 8*a*, 17: 1–30. *Rg.*

***Menetrié, —.** (**1850?**). "Catalogue raisonné des animaux du Caucase."

***Menzbir, M. A.** (**1882**). ["Ornithological geography of European Russia."] Sci. Mem. Moscow Univ. *R.*

*Menzbir, M. A. (1912). ["Zoogeographical atlas."] Moscow. *R.*

Menzbir, M. A. (1934). ["An outline of the history of the fauna of the European part of the U.S.S.R."] Moscow and Leningrad. 223 pp. *R.*

§Middendorff, A. T. (1875). "Reise in dem äussersten Norden und Osten Siberiens. Vol. 4. Part 2. Die Thierwelt Siberiens." St Petersburg.

Minin, N. V. (1936). ["On the question of the subdivision of the arena of life in ecology."] Probl. Ecol. Biocenol. 3: 61–7. *Re.*

*Mittel'man, S. Ya. (1931). ["Die Wissenschaftliche Forschungsstation für Fischerei an der Ostmurmanküste und die 1927–1929 daselbst ausgeführten Arbeiten."] Rep. Inst. Investig. Siberia, 48: 3–18. *Rg.*

Morosova-Vodyanitzkaya, *see* Vodyanitzkaya, Morosova-.

Muraveiskii, S. D. (1937). ["Twenty years of Soviet hydrobiology."] Zool. Zh. 16: 821–9. *R.*

Naumov, N. P. (1934). ["Die Saugetiere des Tungusska-Bezirks."] Rep. Polar Commission Acad. Sci. U.S.S.R. 17: 5–82. *Rg.*

†Naumov, N. P. (1936). ["On some peculiarities of ecological distribution of mouse-like rodents in southern Ukraine."] Zool. Zh. 15: 674–96. *Re.*

Nefedov, N. I. (1930). ["A quantitative study of the ant population of the Irkutsk (Troitsk) forest steppe reserve."] Bull. Inst. Rech. Biol. Perm, 7: 259–91. *Re.*

Nefedov, N. I. (1933). ["Zur Heuschreckenfauna des Kustanaj Distrikt (N.W. Kasakstan) und ihre Verteilung nach Biotopen."] Bull. Inst. Rech. Biol. Perm, 8: 151–88. *Rg.*

Nefedov, N. I. (1933). ["Über die Phänologie der wichtigsten Heuschrekenarten in den Umgebungen von Kustanaj (N.-W. Kasakstan)."] Bull. Inst. Rech. Biol. Perm, 8: 189–204. *Rg.*

Nefedov, N. I. (1933). ["Über die Ökologie der Eikapseln der Heuschreken (Locustoidea) und die Methode zur Abundanzbestimmung derselben."] Bull. Inst. Rech. Biol. Perm, 8: 205–22. *Rg.*

Nefedov, N. I. (1936). ["Contribution to the ecology of Acrididae of some districts adjacent to the Urals. The Acrididae of the Troitsk forest-steppe reserve."] Bull. Inst. Rech. Biol. Perm, 10: 151–78. *Re.*

Nikitin, P. A. (1926). ["Synecologische Beobachtungen am Woronesh-Flusse."] Arb. Allruss. Bot. Kongr. Moscow: 133–4. *R.*

*Nikitin, V. N. (1926). ["La distribution verticale du plancton dans la Mer Noire. 1. Copepoda et Cladocera."] Trav. Sta. Biol. Sebastopol, 2: 93–140. *Rf.*

Nikitin, V. N. (1929). ["La distribution verticale du plancton dans la Mer Noire. II. Zooplancton (les copépodes et les cladocères exceptés)."] Trav. Sta. Biol. Sevastopol, 1: 27–152. *Rf.*

Nikitin, V. N. (1938). "The lower limit of the bottom fauna and its distribution in the Black Sea." C.R. Acad. Sci. U.R.S.S. 21: 335–9. *E.*

Nikitin, V. V. (1933). ["The soils of the Transural forest steppe zone and a general description of its natural conditions."] Trav. Inst. Rech. Biol. Perm, 5: 1–227. *Re.*

Nikitin, V. V, & Maladin, G. A. (1928–30). ["The soil and vegetation of the Troitsk district, Ural province."] Trav. Inst. Rech. Biol. Perm, 2: 3, 109–356, 357–388, and 389–430. *Re.*

§*Nordmann, — (1833). "Faune pontique. Voyage de Demidoff." vol. 3.

Obolenskii, S. I. (1931). ["A plan for the study of terrestrial vertebrates in the U.S.S.R. to be carried out by plant protection institutions."] Bull. Pl. Prot. Leningr. Ser. 4, 1: 95–101. *Re.*

Ognev, S. I. (1928, 1931, 1935). ["The mammals of Eastern Europe and Northern Asia."] Moscow and Leningrad. Vols. 1–3. *R.*

Ognev, S. I. (1935). ["The Laboratory of Vertebrate Zoology and its work in 1932."] Miscellany Inst. Zool. Moscow St. Univ. 2: 38–42. *Re.*

Ognev, S. I. (1936). ["The work of the Laboratory of Vertebrate Zoology in 1933."] Miscellany Inst. Zool. Moscow St. Univ. 3: 77–9. *Re.*

*Orlov, E. I. & Lonzinger, G. K. (1937). ["On the methods of the quantitative study of small forest mammals."] Sci. Rep. Saratov St. Univ. 1 (14): 165–75. *R.*

Ostroumov, N. A. (1927). ["An essay on the ecology of sometimes flooded woods."] Proc. Russ. Congr. Zool. 2: 46–7. *R.*

*Ostroumov, N. A. (1936). ["The fishes and fisheries of the Piasina River."] Rep. Polar Commission Acad. Sci. U.S.S.R. 30: 1–115. *Re.*

Oushakov, *see* Ushakov.

Pavlovskii, E. N. (**1937**). ["Biocenological studies as applied to parasitological problems."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1385–422. *Re.*

Pavlovskii, E. N. (**1937**). ["Expeditionary works of the Zoological Institute of the Academy of Sciences of the U.S.S.R. in 1931–1936."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1613–30. *Re.*

Pavlovskii, E. N. & Filip'ev, N. N. (**1935**). ["A short review of the All-Russian Entomological Society during the 75 years of its organisation (1860–1935)."] Rev. Ent. de l'U.R.S.S. 26: 3–14. *R.*

Pazhitnova, Z. A. (**1929, 1935**). ["Materials on the microfauna of rice fields and the biology of the larvae of *Anopheles* in rice fields."] Acta Univ. Asiae Med. Ser. 8*a*, 10: 1–40; 18: 1–64. *Rg.*

§**Pelts, V.** (**1928**). "Some aspects of forestry in Russia." Indian Forester, 54: 215–25, 290–301, 349–61, and 406–11.

Pereleshina, V. I. (**1928**). ["Fauna of spiders in the environs of the biological station at Bolchevo."] Bull. Sta. Biol. Bolchevo, 2: 1–74. *Re.*

***Pershakov, A. A.** (**1929**). ["Changements survenus dans l'ornithofauna du pays de Kazan pour period de 1896–1929."] Bull. Agr. and For. Inst. Kazan, 2: 91–126. *Rf.*

Petrov, M. P. (**1936**). ["On the ecology of the saltmarsh and sandy saksaouls."] Probl. Ecol. Biocenol. 3: 3–46. *Re.*

Pirozhnikov, P. (**1929**). ["Zur Erforschung des Benthos des Jenessej-Stromes."] Russ. Hydrobiol. Zh. 8: 68–73. *R.*

§**Pleske, T.** (**1928**). "Birds of the Eurasian tundra." Mem. Boston Soc. Nat. Hist. 6: 109–485.

***Plokhotskii, K. Plyater-** (**1936**). ["Materials on the study of succession of mouse-like rodents of Southern districts of the Far Eastern region."] Bull. Far Eastern Br. Acad. Sci. U.S.S.R. (Vladivostok), 16: 175–7. *Re.*

Plyater-Plokhotskii, *see* **Plokhotskii, Plyater-**.

Pokrovskii, S. V. (**1925**). ["Quelques observations faites sur l'habitation des araignées dans les environs de la station biologique de Bolchevo en 1923."] Bull. Sta. Biol. Bolchevo, 1: 19–25. *Rf.*

***Poplavskaya, G. I.** (**1937**). ["The ecology of plants."] Leningrad: BIOMEDGIZ.

Popov, A. M. (**1931**). "Distribution of fishes in the Black Sea with reference to bottom conditions." Ecology, 12: 468–75.

Popov, A. M. (**1935**). "The fauna of Avacha Bay and its distribution into communities." C.R. Acad. Sci. U.R.S.S. 4: 373–6. *E.*

Pospelov, V. P. (**1929**). ["Symbiotic microorganisms in their relation to the diseases of insects."] Plant Protection, Leningr. 6: 13–20. *R.*

Predtechenskii, S. A. (**1928**). ["*Locusta migratoria* L. in Central Russia."] Rep. Bur. Appl. Ent. Leningr. 3: 113–99. *Re.*

Predtechenskii, S. A. (**1928**). ["The locust species (Acrididae, Orthoptera) of the Lower Volga region."] Commentarii Inst. Astrachan. Def. Plant. 2 (1): 1–115. *Re.*

Predtechenskii, S. A. (**1929**). ["Das Ural-Delta in orthopterologischer Hinsicht."] Rep. Bur. Appl. Ent. Leningr. 4: 219–23. *Rg.*

***Predtechenskii, S. A.** (**1930**). ["Die Heuschrecke (*Locusta migratoria* L.) in der Rjasano-Tambowscher Niederung."] Bull. Pl. Prot. Leningr. Ser. 1, 3: 3–49. *Rg.*

***Predtechenskii, S. A.** (**1935**). ["The annual cycle of the desert locust (*Schistocerca gregaria* Försk.), its migrations and periodicity in Persia and adjacent countries of tropical and subtropical Asia."] Bull. Pl. Prot. Ser. 1, 12: 1–135. *Re.*

***Predtechenskii, S. A., Zhdanov, S. P. & Popova, A. A.** (**1935**). ["Injurious locusts in U.S.S.R. in the years 1925–1933."] Bull. Pl. Prot. Leningr. Ser 1, 18: 1–167. *Re.*

***Promptov, A. N.** (**1928**). ["The present status of research on migratory birds."] Sci. News U.S.S.R. 6–7: 140–69. *R.*

Promptov, A. N. (**1936**). ["Ecogenetic factors in the evolutionary divergence of birds."] Biol. Zh. 5: 1001–10. *Re.*

Pyatnitzkii, G. K. (**1930**). ["Materials for the study of the bark beetles of the spruce forests of the Poshekhon district in the Yaroslav government."] Plant Protection, Leningr. 6: 595–629. *R.*

Rabotnov, T. A. (**1935**). ["Die natürlichen Regionen des südlichen Teils der Autonomen Sozialistischen Soviet-Republik Jakutien (J.A.S.S.R.)."] Bot. Zh. 20: 177–210. *Rg.*

***Raikova, I. A.** (**1930**). ["The vegetative landscape of the Pamir."] Acta Univ. Asiae Med. Ser. 8*b*, 12: 1–24. *Re.*

§**Rainey, R. C.** (**1938**). "Plant protection in the Soviet Union." Nature, Lond., 141: 756–7.

Rall', Yu. [**M.**] [**G.**] (**1933**). ["List of Russian literature on the role of rodents in the epidemiology of plague and tularaemia in the Volga basin and W. Kazakstan."] Rev. Microbiol., Saratov, 12: 229–39. (Lists 259 references.) *R.*

Rall', Yu. M. (**1936**). ["Some methods of ecological census of rodents."] Probl. Ecol. Biocenol. 3: 140–57. *Re.*

Rall', Yu. M. (**1936**). ["The relation between rodents and the mosaic landscape of the sandy semi-desert."] Zool. Zh. 16: 149–64. *Re.*

Rall', Yu. M., Demyashev, M. & Sheikina, M. (**1936**). ["Periodic phenomena in the biology of the most important rodents of sandy semi-desert territories (West Kazakhstan)."] Rev. Microbiol., Saratov, 15: 380–406. *Re.*

***Regel, C.** (**1932**). "Pflanzensoziologische Studien aus dem nördlichen Russland. I. Die Flechentundra von Nowaja Semlja [Novaya Zemlya]." Beitr. Biol. Pfl. 20: 7–24.

***Regel, C.** (**1933**). "Pflanzensoziologischen Studien aus dem nördlichen Russland. II. Die "Tundra" am Südufer des Weissen Meeres und das Problem der sekundären Tundren." Beitr. Biol. Pfl. 21: 117–31.

***Regel, C.** (**1935**). "Pflanzensoziologischen Studien aus dem nördlichen Russland. III. Die Reliktenvereine in der Arktis." Beitr. Biol. Pfl. 23: 105–21.

Reingard, L. V. & Gutzevich, A. V. (**1931**). ["Notes on the ecology of mosquitoes."] Mag. Parasitol. U.S.S.R. 2: 119–34. *R.*

Resvoi, P. D. (**1924**). ["Zur Definition des Biocönose-Begriffs."] Russ. Hydrobiol. Zh. 3: 204–9. *Rg.*

Retovskii, L. O. (**1928**). ["Hydrobiology and plankton of the drying brackish lake in the Kalmuck steppe."] Proc. Russ. Congr. Zool. 3: 377–8. *R.*

Rimskii-Korsakov, *see* **Korsakov, Rimskii-.**

Rodin, L. E. (**1933**). ["The types of steppe of the lower Trans-Volga region."] Bot. Zh. 18: 299–306. *Rg.*

Rodionov, Z. S. (**1937**). ["Conditions for mass development of grain mites."] Zool. Zh. 16: 511–46. *Re.*

***Rodionov, Z. S.** (**1937**). ["On the habits and spreading of grain mites."] Zool. Zh. 16: 1013–21. *Re.*

***Romashov, D. D.** (**1931**). ["On the condition of "equilibrium" in populations."] J. Biol. Exp. Moscow, 7: 442–54. *R.*

***Rubtzov, I. A.** (**1932**). ["Food plants of Siberian Acrididae."] Bull. Pl. Prot., Leningr. Ser. 1, 3: 13–31. *Re.*

***Rubtzov, I. A.** (**1932**). ["The habits and conditions of grasshopper outbreaks in E. Siberia."] Bull. Pl. Prot., Leningr. Ser. 1, 3: 33–130. *Re.*

***Rubtzov, I. A.** (**1932**). ["On the estimation of the actual density of the grasshopper population by the method of sweeping."] Plant Protection, Leningr.: 69–80. *R.* (English abstract in Rev. Appl. Ent. A, 21: 51–2.)

Rubtzov, I. A. (**1933**). ["Materials on the ecology of injurious locusts in eastern Siberia."] Bull. Pl. Prot. Siberia: 8–97. *R.*

***Rudnev, D. F.** (**1933**). ["Materialen zur Oekologie von *Lophyrus pini* L. im Zusammenhang mit den Besonderheiten seiner Verbreitung in Waldbeständen."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 1: 135–44. *Ug.*

Rudnev, D. F. (**1935**). ["Methoden zur Feststellung der Befallstärke der Kieferneule (*Panolis flammea* Schiff.)."] Trav. Inst. Zool. Biol. Acad. Sci. Ukr., Kiev, 2: 57–134 and 259–63. *Urg.*

Ruilov [Rylov], V. M. (**1925**). ["Chloro-bioseston in the waters near Peterhof."] Russ. Hydrobiol. Zh. 4: 84–95. *Rg.*

Ruilov, V. M. (**1927**). ["Studien über das Teichplankton der Umgebung des Peterhofer Naturwissenschaftlichen Instituts."] Trav. Inst. Sci. Peterhof, 4: 1–253. *Rg.*

***Ruilov [Rylov], V. M.** (**1935**). "Das Zooplankton der Binnengewässer." Stuttgart.

Ruilov, V. M. (**1937**). ["Investigations of zooplankton in the continental waters of U.S.S.R. during the 20 years following the great October Revolution (1917–1937)."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1631–40. *Re.*

***Rule, K. F.** (**1852**). ["The life of animals in relation to external conditions."] Moscow. *R.*

***Sakharov, N. & Strukov, V.** (**1927**). ["The study of the nocturnal insect fauna, particularly of the Noctuidae."] J. Exp. Landw. Südost. Eur.-Russ. 4 (2): 249–62. *Rg.* (English abstract in Rev. Appl. Ent. A, 16: 151.)

***Samoilov, T. P.** (**1936**). ["Materials on the bio-ecology of the wood beetles of the S. Ussuriisk district."] Trans. Mt. Sta. Far East. U.S.S.R. 1: 217–38. *R.* ♯

Savik, N. P. Durymanova- (**1936**). ["Contribution to the ecology and biology of rodents of the Troitsk district, formerly Ural province: some observations on the character of food of some rodents."] Bull. Inst. Rech. Biol. Perm, 10: 101–13. *Re.*

***Savitzkii, G. G.** (**1936**). ["The Biological Scientific Research Station at the Rostov-on-Don University."] Priroda, 8: 130–1. *R.*

Schalyt, *see* **Shalit.**

Schennikow, *see* **Shenikov.**

§Seifriz, W. (**1931–32**). "Sketches of the vegetation of some southern provinces of Soviet Russia. I–V." J. Ecol. (1931) 19: 360–82; (1932) 20: 53–88.

§Seifriz, W. (**1934**). "The plant life of Russian Lapland." Ecology, 15: 306–18.

***§Seifriz, W.** (**1936**). "Vegetation zones in the Caucasus." Geogr. Rev. 26: 59–66.

***Seredrovskii, P. V.** (**1935**). ["The history of the Russian animal world."] Leningrad. *R.*

Sergeev, A. (**1936**). "L'influence des constructions de l'homme sur la distribution des oiseaux dans les steppes." C.R. Acad. Sci. U.R.S.S. 2: 165–8. *F.*

***Severtzov, N. A.** (**1855**). ["Periodic phenomena in the life of the mammals, birds and reptiles in the Voronezh District...."] Moscow. *R.*

***Severtzov, N. A.** (**1877**). ["On the zoological preference for ornithological regions in the non-tropical parts of our mainland."] Proc. Russ. Geogr. Soc. 13. *R.*

***Severtzov, N. A.** (**1879**). ["The vertical and horizontal distribution of the animals of Turkestan."] Moscow. *R.*

Severtzov, S. A. (**1933**). ["Zum Problem der Herde bei den Wirbelthieren."] Bull. Acad. Sci. U.R.S.S.: 1005–46. *Rg.*

Severtzov, S. A. (**1934**). "On the dynamics of populations of vertebrates." Quart. Rev. Biol. 9: 409–37.

Severtzov, S. A. (**1934**). "Vom Massenwechsel bei den Wildtieren." Biol. Zbl. 54: 337–64.

Severtzov, S. A. (**1935**). ["Zur Frage der Vermehrungsbiologie der Tetraoniden im staatlichen Waldschutzgebiet Baschkiriens...."] Zool. Zh. 14: 371–96. *Rg.*

Severtzov, S. A. (**1937**). ["Darwinism and ecology."] Zool. Zh. 16: 591–613. *R.*

Shadin, W. I. (**1935**). "Über die ökologische und geographische Verbreitung der Süsswasser-mollusken in der U.d.S.S.R." Zoogeographica, 2: 495–554.

Shalit [Schalyt], M. S. & Kalmykova, A. A. (**1935**). ["Steppenbrände und deren Einfluss auf die Vegetation."] Bot. Zh. 20: 101–10. *Rg.*

Sharleman', N. V. [Charlemagne, M.] (**1923**). [Essay on the division of Ukraine into zoo-geographical regions.] Proc. Russ. Congr. Zool. 1: 38–9. *R.*

***Sharleman', M. V. [M.]** (**1926**). ["Zoogeographical regions of Ukraine."] Mem. Phys.-Mat. Acad. Sci. Ukr. 2: 137–48. *U.*

Sharleman', M. V. (**1937**). ["Zoogeography of U.S.S.R. Materials for the study of the geographical distribution of land vertebrates in the Ukr. S.S.R."] Kiev: Acad. Sci. 234 pp. *Ure.*

Shchegolev, V. N. (**1936**). ["Ecologo-economic zonation of the U.S.S.R. territory in relation to agricultural pests and diseases of plants."] Summ. Sci. Res. Work, Inst. Pl. Prot. Leningr. 1935: 11–13. *R.*

§Shelford, V. E. (**1934**). ["Life zones and modern ecology."] Probl. Ecol. Biocenol. [1]: 3–15. *Re.*

Shenikov [Schennikow], A. P. (**1934**). ["Was ist Geobotanik? (Zur Metodologie der Geobotanik)."] Bot. Zh. 19: 393–401. *Rg.*

Shenikov, A. P. (**1935**). ["Über das monographische Studium der taxonomischen Vegetationseinheiten."] Bot. Zh. 20: 414–8. *Rg.*

Sherbakov, A. P. & Kuznetzov, S. I. (**1927**). ["Distribution of the microfauna and microflora in swamps and its dependence on the physico-chemical factors."] Proc. Russ. Congr. Zool. 2: 303–4. *R.*

Shiperovich, V. Ya. (**1937**). ["Soil fauna in different types of forest."] Zool. Zh. 16: 301–10. *Re.*

Shirshov, P. (**1935**). ["Plankton as an indicator of the ice regime of the sea."] Bull. Arctic Inst. U.S.S.R. (11): 376–7. *R.*

Shtegman, B. K. (**1937**). ["Progress of Soviet ornithology during the period 1917–1937."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1641–66. *Re.*

Simanovskaya, V. G. (**1937**). ["Zoological literature of U.S.S.R. (chiefly for 1936)."] Zool. Zh. 16: 1022–77. *R.* (The references collected for the *Zoological Record.*)

***Siyazov, M. M.** (**1936**). ["Work on the ecology of the region of the Zarevshank floodplain." Trans. Uzbekistan St. Univ. 7: 9–24. *R.* ♯

***Siyazov, M. M.** (**1936**). ["Preliminary characterisation of the biocenoses of the Zaravshanks floodplain."] Trans. Uzbekistan St. Univ. 7: 25–41. *R.* #

Skadovskii, S. N. (**1935**). ["The Laboratory of Hydrobiology in 1932."] Miscellany Inst. Zool. Univ. St. Moscow, 2: 14–15. *R.*

***Skadovskii, S. N.** (**1937**). ["Work of the Laboratory of Hydrobiology and the Zvenigorod Hydrophysiological Station in 1933."] Miscellany Zool. Inst. Moscow Univ. 3: 18–20. *R.*

Smaragdova, N. P. (**1936**). ["The interaction between phytophagous and predatory mites in relation to their environment and concentration."] Zool. Zh. 15: 720–30. *Re.*

Smaragdova, N. P. (**1937**). ["Some observations and experimental investigations on the dynamics of periphytone biocoenoses."] Zool. Zh. 16: 280–300. *Re.*

Smelov, S. P. (**1936**). ["Der Wiesen-Sumpf-Komplex auf der Wasserscheide der Wolga, des Dnjepr und des Ilmensees."] Bot. Zh. 21: 206–30. *R.*

Smirnova, Z. N. (**1928**). ["Die Waldassoziationen des nord-westlichen Teiles des Leningrader Gebietes (Kreis Kingissepp, ehemals Jamburg)."] Trans. Inst. Sci. Peterhof, 5: 119–264. (Contains a good succession chart.) *Rg.*

Stanchinskii, V. V. (**1923**). ["The ecological principle in zoogeography: the problems of ecological and geographical investigations of the ornithofauna."] Proc. Russ. Congr. Zool. 1: 29–30. *R.*

Stanchinskii, V. V. (**1923**). ["Zoogeographical concepts of stations and work on the classification of stations of birds in central Russia."] Proc. Russ. Congr. Zool. 1: 29–30. *R.*

Stanchinskii, V. V. (**1927**). ["Some climatic factors influencing the distribution of birds."] Proc. Russ. Congr. Zool. 2: 62–4. *R.*

Stanchinskii, V. V. (**1927**). ["The ecotropic factors as a special category of factors in distribution of birds."] Proc. Russ. Congr. Zool. 2: 64–5. *R.*

Stanchinskii, V. V. (**1931**). ["Zur Frage der Bedeutung der Masse der Artensubstanz für das dynamische Gleichgewicht der Biocönosen."] J. Ecol. Biocenol. 1: 88–98. *Rg.*

Stanchinskii, V. V. (**1931**). ["The method of quantitative study of grass associations."] J. Ecol. Biocenol. 1: 133–7. *Re.*

Stankov, S. S. (**1933**). ["Principal features of vegetation distribution in southern Crimea."] Bot. Zh. 18: 66–94. *Re.*

***Stark, N. K.** (**1931**). ["The insect fauna of different types of forest."] Plant Protection, Leningr. 7: 339–43. *R.* (English abstract in Rev. Appl. Ent. A, 20: 232–3.)

Stark, V. N. (**1926**). ["The influence of soil on the injurious insect fauna of poplar."] Plant. Protection, Leningr. 3: 15–22. *R.*

Stark, V. N. (**1926**). ["The influence of *Platysoma oblongum* F. on the development of *Myelophilus* (*Blastophaga*) *piniperda* L. in pine stumps."] Plant Protection, Leningr. 3: 339–42. *R.*

***Stark, V. N.** (**1929**). ["On the formation of bark beetle associations under the influence of the density of forest."] Plant Protection, Leningr. 6: 389–98. *R.* (English abstract in Rev. Appl. Ent. A, 18: 669.)

***Stark, V. N.** (**1930**). ["Methods of investigation of the insect fauna of forest soils. I. The importance of the soil strata."] Plant Protection, Leningr. 6: 763–72. *R.* (English abstract in Rev. Appl. Ent. A, 19: 46–7.)

***Stark, V. N.** (**1936**). ["Survey of the work on forest entomology, as illustrated in the Leningrad district in the period from 1842 to 1934."] Leningrad: Acad. Agr. Sci. *R.* #

Startzeva, F. V. & Glumov, G. A. (**1936**). ["Contribution to the ecology and biology of rodents of the Troitsk district, formerly Ural Province. 4. Influence of farming on the spread of rodents of steppe stations."] Bull. Inst. Rech. Biol. Perm, 10: 125–43. *Re.*

Strakhovskii, A. N. (**1935**). ["Materials for the ecological characterisation of the Acrididae of the Kuznetzk steppe."] Bull. W. Sib. Pl. Prot. Sta. Novosibirsk, 1 (9): 71–118. *R.*

Sukachev [Sukatschev], V. (**1918**). ["On the terminology in the investigation of plant communities."] Zh. Russ. Bot. Soc. 2: Appendix 1–19. *R.*

***Sukachev, V. N.** (**1925–6**). "Über die Methoden der Phytosoziologie." Engler's Bot. Jahrb. 50, Beibl. 135: 1–6.

***Sukachev, V. N.** (**1928**). ["Plant communities."] Moscow. *R.*

Sukachev, V. N. (**1928**). "Principles of classification of the spruce communities of European Russia." J. Ecol. 16: 1–18.

***Sukachev, V. N.** (**1929**). "Über einige Grundbegriffe in der Phytosoziologie." Ber. Deutsch Bot. Ges. 1929.

†**Sviridenko, P. A.** (**1934**). ["Increase and decrease of population of mouse-like rodents."] Bull. Pl. Prot., Leningr. Ser. 4, 3: 1–60. *Re.*

Sviridenko, P. A. (1936). ["Study of the laws concerning the mass outbreaks of murine rodents."] Summ. Res. Work, Inst. Pl. Prot. Leningr. for 1935: 74. *R.*

Sviridenko, P. A. (1936). ["Rodents of the North Caucasus and of the Ciscaucasian steppes."] Miscellany Inst. Zool. Moscow St. Univ. 3: 86–9. *R.*

Tauson, A. O. (1934). ["Hydrobiologische Untersuchungen über die Seen der Ober-Kama."] Trav. Inst. Rech. Biol. Perm, 6: 103–19. *Rg.*

Tcheterkina, *see* **Chetuirkina.**

Tchugunoff, *see* **Chugunov.**

***Tiflov, V. (1936)** ["Bibliography on the fleas of U.S.S.R."] Rev. Microbiol., Saratov, 14: 131–41. *R.*

Tolmachev, A. (1932). ["On an attempt at classification of types of tundra."] Bot. Zh. 17: 329–31. *R.*

Trefilova-Zinovyeva, *see* **Zinovyeva, Trefilova-.**

***Troitzkii, N. N. (1929).** ["Some results of comparative ecological studies on *Phylloxera* in U.S.S.R."] Bull. St. Inst. Exp. Agron. (GIOA), 7 (3): 1–24. *R.*

Tzeeb, Ya. Ya. (1937). ["On methods of quantitative evaluation of the Pelogen microfauna in connection with its application to saline lakes of the Crimea."] Zool. Zh. 16: 499–511. *Re.*

Ushakov [Oushakov], P. V. (1925). ["Seasonal investigations on the littoral of the Kolsk Bay."] Trav. Soc. Nat. Leningr. 54: 47–72. *Rf.*

Ushakov, P. V. (1928). ["Floro-faunistic groups of the coast zone of Novaya Zemlya."] Proc. Russ. Congr. Zool. 3: 383–5. *R.*

Various authors (1934). ["Fauna and ecology: materials for the investigation of the nature of the Western regions."] The Western Regional State Publishers. Smolensk and Moscow. 140 pp.

Various authors (1936). ["Summary of the scientific research work of the Institute of Plant Protection for the year 1935."] Lenin Acad. Agric. Sci., Inst. Plant. Prot., Leningr. 546 pp. *R.* (English abstract in Rev. Appl. Ent. A, 25: 137–60.)

Veitzman, Kh. S. [Weizmann, X. C.] (1936). ["Concerning some biocoenological concepts."] Probl. Ecol. Biocenol. 3: 68–78. *Re.*

Vereshchagin [Vereschagin], G. Yu. (1923). ["Zur Frage der Biocoenosen und Stationen im Gewassern."] J. Russ. Bot. Soc. 2 (3/4): 53–64. *Rg.* (Abstract in Russian only in Proc. Russ. Congr. Zool. 1: 45–6.)

Vereshchagin, G. Yu. (1927). ["Bibliography on Lake Baikal and its littoral zone."] Trav. Comm. Lac Baikal, 2: 187–222. (Supplement for literature 1927–31 published in 1933, Trav. Limnol. Sta. Lac Baikal, 5: 162–178.) *R.*

Vereshchagin, G. Yu. [J.] (1935). ["Zwei Typen der biologischen Komplexe des Baikalsees."] Trav. Sta. Limnol. Lac Baikal, 6: 199–212. *Rg.*

***Vernadskii, V. I. (1926).** ["The biosphere."] Leningrad. *R.*

Vinberg, G. (1936). ["Some general problems concerning the productivity of lakes."] Zool. Zh. 15: 587–603. *Re.*

Vindelbandt, A. A. (1933). ["List of the publications of the Institute of Plant Industry, 1908–1931."] Bibliogr. Contr. 2, Inst. Pl. Ind., Leningrad. pp. 1–182. *R.*

Vinogradov, B. S. (1934). ["Materials for the study of the dynamics of the fauna of muriform rodents in U.S.S.R. (Historical review of fluctuations of mice in U.S.S.R.)."] People's Commissariat of Agriculture, Assoc. for Pest and Diseases Control in U.S.S.R., Record Service. Leningrad. 62 pp. *R.*

***Vinogradov, B. S. (1935).** ["Animal life of deserts."] In "Turkmania", Acad. Sci. U.S.S.R. 1934: 364–73. *R.*

Vinogradov, B. S. (1937). ["Works of the Zoological Institute on the study of mammals of Middle Asia."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1142–8. *Re.*

Vinogradov, V. S. and others (1937). ["A brief review of investigations performed on mammals in U.S.S.R. for 20 years (1917–1937)."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1503–13. *Re.*

Vinokurov, G. M. (1927). ["Grasshoppers and the areas of their mass occurrence in eastern Siberia. Preliminary note."] Bull. Irkutsk Pl. Prot. Sta. 1: 3–52. *Re.*

Vinokurov, G. M. & Rubtzov, I. A. (1930). ["Studies on the ecology of grasshoppers in the Irkutsk district."] Bull. Irkutsk Pl. Prot. Sta. 2: 3–86. *Re.*

Vladimirskii, A. P. (1923). ["The results of a census of the fauna of single plants."] Proc. Russ. Congr. Zool. 1: 18–20. *R.*

Vladimirskii, A. P. (1925). ["Results of a quantitative survey of the fauna of individual plants. I. A count of the fauna inhabiting the leaves of trees."] Trav. Soc. Nat. Leningr. 55: 111–36. *Rg.*

Vladimirskii, A. P. (1926). ["Ergebnisse quantitativer Zählungen der Fauna an einzelnen Pflanzen. II. Quantitative Zählung der auf Kräutern lebenden Tierwelt. III. Quantitative Zählung der Blütenfauna (Anthobium nach der Terminologie von V. Dogiel)."] Trav. Inst. Sci. Peterhof, 3: 99–168. *Rg.*

Vladimirskii, A. P. (1927). ["A quantitative account of the fauna of fruits."] Proc. Russ. Congr. Zool. 2: 310–11. *R.*

***Vladimirskii, A. P. (1928).** "Versuch einer quantitativen Zählung der Beerenfauna (Materialien zu einer quantitativen Zählung der Fruchtfauna)." Z. Morph. Ökol. Tiere, 11: 235–46.

Voblikova, T. (1926). ["Oekologische Reihen der Meereswiesen-Associationen auf der Insel Bolschoy Oleniy in dem Kola Fjorde."] Trav. Biol. Sta. Murman, 2: 93–105. *Rg.*

Vodyanitzkaya, N. Morozova- (1936). ["Essai d'une évaluation quantitative de la végétation du fond de la Mer Noire."] Trav. Sta. Biol. Sebastopol, 5: 45–217. *Rf.* (French summary 10 pp.)

Vodyanitzkaya, N. Morosova- (1936). ["Phytobenthos des Karkinitzky Busens."] Trav. Sta. Biol. Sebastopol, 5: 219–32. *Rg.*

Vodyantzkii, V. A. (1937). ["Progress in the study of the Black Sea."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1515–26. *Re.*

***Vorob'ev, D. P. (1936).** ["The mountain station of the Far-Eastern Filial of the Academy of Sciences U.S.S.R. and the Preserve for Ussuriisk flora and fauna."] Trans. Mt. Sta. Far East. U.S.S.R. 1: 9–13. *R.* ♯

Voronov [Woronoff], A. G. (1935). ["Quelques observations sur l'action du campagnol vivant en société (*Microtus socialis* Pall.) sur les pâturages situés au pied des montagnes du Daghestan."] Bull. Soc. Nat. Moscou, Sect. Biol. 44: 314–23 and 391–406. *Rf.*

Voronov, A. G. (1935). ["The effect of winter activity-habits of the vole on pasture plants."] Sovietsk. Bot. 71–83. *R.*

***Vorontzov, E. M. (1936).** ["Essay on the ecological ana ysis of the ornithofauna of the Kachischsko-Krilovsky Forestry of the Briansk woodlands massive."] Proc. Zool. Biol. Inst. Kharkov Univ. 1: 230–58. *Ue.*

***Vul'f [Wulff, Wolf], E. V. (1932).** ["Introduction to the historical geography of plants."] Moscow: SELKHOZGIZ. *R.*

Vul'f, E. V. (1934). ["A survey of the literature of the last 16 years on the development of the flora of the U.S.S.R."] Bot. Zh. 19: 64–100. *R.*

***§Warming, E. (1901).** ["Ecological geography of plants."] (Russian translation of "Plantesamfund" ["Oecology of plants"].) Moscow.

Weizmann, X. C., *see* **Veitzman, Kh. S.**

Woronoff, *see* **Voronov.**

Wulff, *see* **Vul'f.**

Yaguzhinskii, S. N. (1929). ["Flora und Pflanzenassoziationen des Flusses Kljasma."] Bull. Sta. Biol. Bolchevo, 3: 122–33. *Rg.*

Yakubova, F. I. (1935). ["The division into districts of the Black Sea on the basis of composition and distribution of its benthal fauna."] C.R. Acad. Sci. U.R.S.S. 1: 261–7. *Re.*

Zachs, I. (1929). ["Upon the bottom communities of the Shantar Sea (S.W. Okhotsk Sea)."] Bull. Pacific Fish Res. Sta. 3 (2): 1–112. *Re.*

Zeeb, J., *see* **Tzeeb, Ya.**

***Zenkevich [Zenkewitch], L. A. (1927).** ["Quantitative investigations of the bottom fauna of Petchore region of the Barents Sea and of the White Sea."] Bull. Oceanogr. Inst. Moscow, 2 (4): 1–64. *Re.*

***Zenkevich, L. A. (1930).** ["A quantitative evaluation of the bottom fauna in the sea region about the Kanin peninsula."] Bull. Oceanogr. Inst. Moscow, 4 (3): 7–23. *Re.*

Zenkevich, L. A. (1937). ["The achievements in the study of the marine fauna of the U.S.S.R. for 20 years."] Zool, Zh. 16: 830–70. *R.*

***Zenkevich, L. A. & Brotzkii, V. (1932).** ["A quantitative evaluation of the bottom fauna of Cheshskaya Bay."] Bull. Oceanogr. Inst. Moscow, 2 (2): 41–57. *Re.*

*__Zenkevich, L. A. & Brotzkii, V.__ (__1937__). ["Some data on the ecology of dominants in the benthos of the Barents Sea."] Wiss. Ber. Moskau. St. Univ. 14: 203–26. *Re.*

*__Zenkevich, L. A., Brotzkii, V. & Idelson, M.__ (__1928__). "Materials for the study of the productivity of the sea bottom in the White, Barents and Kara Seas." J. Cons. Int. Explor. Mer, 3 (3): 371–79.

__Zernov, S. A.__ (__1921__). ["Versuch einer synchronisteschen Tabelle zur Entwicklungsgeschichte der Hydrobiologie, Ichthyologie, und anderer nahestehender Wissenschaften."] Russ. Hydrobiol. Zh. 1: 1–7. *Rg.*

*__Zernov, S. A.__ (__1934__). ["General hydrobiology."] Moscow and Leningrad. *R.*

__Zernov, S. A.__ (__1937__). ["The Zoological Institute of the U.S.S.R. Academy of Sciences in the period 1931–1936."] Bull. Acad. Sci. U.R.S.S. (Ser. Biol.): 1121–41. *Re.*

*__Zhdanov, S.__ (__1934__). ["The Moroccan locust (*Dociostaurus maroccanus* Thnb.) in the Stavropol province (N. Caucasus)."] Bull. Pl. Prot., Leningr. Ser. 1, 9: 3–51. *Re.*

*__Zimin, L.__ (__1934__). ["On the biology and ecology of *Calliptamus turanicus* Tarb. in Central Asia."] In Predtechinskii and others, 1935: 82–112. *R.*

__Zinovyeva, L. A. Treflova-__ (__1935__). ["A short description of the vegetation of the Troitsk Forest-Steppe Reserve."] Bull. Inst. Rech. Biol. Perm, 9: 381–404. *Re.*

*__Znamenskii, A. V.__ (__1927__). ["Instructions for carrying out observations on the entomofauna of the soil."] Trans. Poltava Agric. Expt. Sta. 51 (14): 1–58. *R.*

__Zolotarev, E. Ch.__ (__1936__). ["On the causes of the mass appearance of the migratory locust (*Locusta migratoria*) in the Western Province in 1933 and of its disappearance in 1934."] Miscellany Inst. Zool. Moscow St. Univ. 3: 197–218. *Re.*

__Zubareva, S. P.__ (__1930__). ["Statistical evaluation of the method of quantitative entomological collection by sweep nets."] Trav. Inst. Rech. Biol. Perm, 7: 89–104. *Re.*

*__Zverev, M. D.__ (__1931__). ["Materials on the biology and agricultural significance in Siberia of the polecat and other small predators of the family Mustelidae."] Bull. Pl. Prot. Siberia, 1 (8): 5–45. *R.*

REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 27, No. 2, August 1939)

THIS number contains eleven papers, an appreciation of the late Prof. Carl Schröter and the individual contributions to a symposium. With eight reviews, eight notices of vegetation and an account of the Easter meeting of the British Ecological Society, the number includes 287 pages altogether.

There are two contributions of special general interest: first, the Presidential Address to the Ecological Society by Prof. A. G. Tansley on British Ecology during the last Quarter Century: the Plant Community and the Eco-system; and secondly, seven contributions to a symposium on the Reciprocal Relationship of Ecology and Taxonomy. The various contributions to this symposium, following an introduction by A. G. Tansley, are: An ecologist appreciates and criticizes the taxonomist, by E. J. Salisbury; The use of ecological data in taxonomy, by O. W. Richards; Ecology and taxonomic differentiation, by J. S. Huxley; Detailed taxonomy and autecology, by D. H. Valentine; The measurement of ecological factors of use in taxonomy, by C. Diver; Ecology and taxonomy: the taxonomist's viewpoint, by V. S. Summerhayes and W. B. Turrill. A summary of a discussion which followed is also given.

Three papers deal with vegetation overseas. R. E. Vaughan and P. O. Wiehe continue their work on the vegetation of Mauritius with a description of the effect of environment on certain features of leaf structure, while A. P. G. Michelmore contributes a very extensive series of observations on tropical African grasslands. Also dealing with African vegetation but with that of Southern Nigeria alone, is the study by G. C. Evans on the atmospheric environmental conditions in the rain forest of that area. Another study of environmental factors is given in a paper by W. H. Pearsall and C. H. Mortimer on oxidation-reduction potentials in waterlogged soils, natural waters and muds.

Papers dealing with British vegetation include one on the ecology of a raised bog near Tregaron, Cardiganshire, by H. Godwin and V. M. Conway; another on the early growth of beech seedlings under natural and experimental conditions, by J. L. Harley; and a third, by E. Wyllie Fenton, on the vegetation of "screes" in certain hill grazing districts of Scotland. T. M. Harris briefly records changes in fenced grasslands in Wales and Dorothy C. Gibb describes the algal communities of Great Cumbrae in the Firth of Clyde.

In addition to the customary review of the *Journal of Animal Ecology*, reviews deal with British Empire vegetation, the record of the International Phytogeographical Excursion in Morocco and Western Algeria and the vegetation of Nigeria. There are also notices of recent papers on European, British and post-glacial vegetation. W. H. PEARSALL.

AN AMERICAN TEXT-BOOK

A. S. Pearse (1939). *Animal ecology.* 2nd edition, pp. xii + 642, 133 text-figures. McGraw-Hill Publishing Co. Ltd., Aldwych House, London, W.C. 2. Price £1. 10*s*.

The second edition of this well-known work is even longer than the first and there are few branches of zoology on which it does not have at least a word to say. One has the impression that the author finds it so difficult to define a science of ecology that everything is included in case the unknown key were accidentally omitted. As a result there is a certain lack of balance in the book; if some of the subjects dealt with briefly were omitted, the

others could be better treated. But it would be ungracious to complain of receiving too much if everything essential had been included and fully discussed.

The difficulty of writing a satisfactory book on ecology lies in the lack of any agreement as to what the subject is really concerned with. The definition (p. 1) "ecology is the branch of biological science that deals with relations of organisms and environments" would provide the title for an encyclopaedia but does not delimit a scientific discipline. There are three groups of biological facts which in various proportions find a place in most ecological studies. There is first what may be termed systematized natural history, which is very fully treated in the present work. Such subjects as adaptations of colour and behaviour, rhythms, reproductive activities, commensalism, etc., are all discussed with many interesting examples. The second group of facts, in this work mainly treated under the heading "ecological factors", concerns the effects of external stimuli, especially those like temperature, humidity, etc., on animal distribution and behaviour. The discussion of this might be improved. Too many facts belonging to the first group are interpolated and the examples of the quantitative effects of factors might be more numerous and arranged so that generalizations could more easily be made. Finally, there is a third aspect of the subject, the nature and composition of communities, and it is this side of all ecological works which is least satisfactory. This is mainly because far too little examination is made of "nature", while there is far too much description of "composition". Prof. Pearse devotes one page to discussing the "character of communities" whereas 212 pages are occupied by descriptions of "communities". He rightly criticizes those who describe animal communities in terms of dominants, influents, etc., defined only on superficial numerical data. There is usually no evidence at all that a so-called dominant animal has any influence on most of the other species living in the same habitat. On the other hand Prof. Pearse's classification in terms of *a priori* appraisal of physiographic features (e.g. B (*b*) Ponds, (1) Littoral, (*a*) Ponds with bare bottoms, (1) beach above water, (2) surface, (3) shore line, etc.) is open to at least equally strong criticism. It is clear that we do not know enough about the relations of animals to their environment to draw up a logical classification of this sort, and, even if we did, most of these so-called communities would be mere collections of animals which happened to be living near one another.

The reason why the treatment of animal communities is so unsatisfactory is that zoologists have taken over almost unmodified the ideas which they found ready to hand in botany. Amongst plants the competition for growing space ensures that any set of individuals in a small area is necessarily more or less integrated into a real community (i.e. the density of any species effects the densities of the others). In animals where this sort of competition is very little developed quite different principles must be thought out—an exercise still in its very earliest stages. As a general result, botanical ecology is to a considerable extent a science of communities, since almost any spatially defined group of plants is in some sense a community (where, as in the Arctic, vegetation is not continuous, it is notorious that the community concept becomes difficult to apply); in animals, on the other hand, almost the only true communities which have been described are the groups of hosts and parasites or of prey and predators. Whether these relationships alone will prove sufficient to define animal communities is still uncertain.

The chief criticism of the present work therefore is that it is a storehouse rather than a synthesis of existing information. Even as the former it has some disadvantages. The index is very inadequate, the names of authors and animals in particular not being included. Considering that it is a second edition, there are too many misprints (twenty-one have been noticed). It is unfortunate that the author has not usually followed the ordinary convention of printing the Latin names of genera and species in italics, though he has in a few places. The 65 pages of references should prove a useful feature, though they contain an extraordinary number of misprints and mistakes in citation.

O. W. RICHARDS

BIRD BIOLOGY

James Fisher (1939). *Birds as animals.* 281 pp., 10 charts and photographs. William Heinemann Ltd., 99 Great Russell St., London, W.C. 1; and Toronto. Price 12*s.* 6*d.*

It is not usual to find a book, which covers so wide a field so successfully as this one. Every aspect of birds, regarded as objects of zoological research and of amateur bird-watching, is dealt with clearly and concisely in a freely running style which manages to make masses of facts palatable. The two most impressive things about it are the way in which all aspects of bird research are shown to integrate, and the prodigious energy that has gone into the bibliography. For all this the pages do not become unreadable through their burden of references and illustrative names, though some difficulty has been experienced in deciding when and when not to give scientific names.

The first chapter on "Bird historians" and the second on "Bird history" serve to give two introductions to the main part of the book and to emphasize the close relation between the student and the thing studied. "Bird adaptation" (chapter 3) deals quickly with the general systematic state of affairs as regards birds, and finishes with some pertinent remarks on systematic criteria other than morphological ones. In chapter 4 the author passes on to the facts of variation and distribution. Both polymorphism and multiple character clines are dealt with and a rough summary given of the zoogeography of the various groups.

Chapter 5 continues logically to discuss the general effect of the environment and how this may interact with genotypes to produce variation. Also recent work is cited illustrative of limiting factors, whether directly physiological or ecological. A rough classification of major habitats (chapter 6) indicates the vast adaptive radiation of birds and it is shown how communities are zoned, stratified and defined in accordance with each particular set of circumstances.

When we come to the section on bird numbers (chapter 7), one of the most interesting ones to ecologists, we find a little more emphasis placed on the "student", but not at the expense of the "thing studied". Practically all the recent work done on censuses is reviewed and discussed competently (though it is not true to say that "we have no counts of the whole of the breeding population of any British bird cliff", since this has been done for the Isle of May), and the general reader is introduced to recent mathematical work on population equilibria, which he would find difficult to track down in digestible form elsewhere. In chapter 8 migration is summarized most efficiently, though the physiological work is confined to references to Rowan and Bissonnette. Ringing schemes are dealt with shortly.

Perhaps most interesting to the general zoologist is the chapter on colours and display, and this leads on naturally to the two last main chapters on territory and reproduction. In the first the reader is made familiar with modern views on sexual selection and with the important work of Hingston and Huxley on the use and classification of colours. Territory is discussed briefly but accurately and the chapter on reproduction includes the important distinction between ultimate and proximate causes of breeding. A wealth of information also is given on breeding habits and the psychological characteristics of the breeding bird. Finally chapter 12 on "Birds and Man" gives an interesting summary of introductions that have been effected and the efforts that are being made to securing a reasoned attitude towards protection.

The bibliography deserves nothing but praise although a courageous attempt to quote the titles of Aristotle's works in the original Greek has led to a sad mix-up of accents. The illustrations are to the point and a photograph of the author's taken on the Farne Islands deserves special commendation. Even the dust-cover has meaning! H. N. SOUTHERN.

THE RELATION OF MAN TO ANIMALS

F. Fraser Darling (1939). *A naturalist on Rona: essays of a biologist in isolation.* 137 pages, 28 photographs, and folding map. Clarendon Press, Oxford. Price 7*s.* 6*d.*

The organization and following up and digestion of ecological research suck so many ecologists back into the laboratory, the office or the museum, that it is satisfactory to have the observations and thoughts of a man who is constantly engaged upon actual field work and yet does not fall out of touch with the trends of ecological thought. The author, with his wife and son, spent some months on the remote island of North Rona, overcoming with great skill and boldness the considerable difficulties of getting there and living under bad weather conditions. This expedition went chiefly to study the large grey seal herd during its breeding time ashore; but many other subjects were also studied or pondered over, and some of them are described in this book.

Chapters deal with the life of the shore, the display of birds, the island itself and its ancient buildings, the social life of animals, the grey seals, wild life sanctuaries, and deer antlers (from mainland work), and with the feelings evoked by life in wild surroundings. The photographs are of very great beauty, and many are the result of much painstaking work in the field. A solid case is built up for including the social relations in any population study, at any rate of birds and mammals. The connexion between the size of colonies of sea-birds and their reproductive efficiency has already been discussed by the author in another book, and is developed a little further here.

Perhaps the most interesting feature of the present book is the author's outlook upon animal life, acquired and thought out in the course of a great deal of time spent among wild animal populations, and among un-industrialized human ones. These views colour strongly his plans for wild life sanctuaries, and he speaks out boldly upon many issues. On two practical points it is clear that some action should be taken. The legal freedom of the seas enables trippers to shoot sea-birds when they are not actually on land; and the rating laws continue to mulct any landowner who converts his estate into a sanctuary for animal life. Most people would subscribe to the following statement: "Law-making in the interests of wild life should take cognizance of the growing body of ecological work, but the greatest step forward will be when the State establishes wild-life reserves in the more remote parts of the country. They would serve the following public ends immediately: the wild life therein would be given breathing space for a time; the reserve would be a place in which the public could take pride and have healthy enjoyment; research into problems of conservation could be conducted with a scope and continuity of policy impossible at present."

Dr Darling discusses the creation of a Highland sanctuary or National Park. It is greatly to be hoped that when a National Park Authority comes eventually into existence, it will include within its organization some form of Biological Survey, which could coordinate the work of other institutions and of individuals, for the benefit of wild life conservation. How long must the faunal history of this island, and indeed of the British Commonwealth at large, be determined by the casual prejudices of smoking-room discussions or the unavoided clash of material interests? Why not begin to use in an intelligent way the new yardsticks and population concepts of animal ecology?

Dr Darling's essays, written on one of the few almost undisturbed parts of Great Britain, brings up these questions into one's mind, and also, very vividly and sincerely, the "rightness for themselves" of the animals that he describes. The book is very pleasant to read. The writing is at its best when it follows a plain course, and the author need not fear that the reader will flag if he omits some of the icing from his cake. We do not need metaphors about "fairy spears" to visualize the flashing mackerel in its course. Will not the clear vigorous language of Gilbert White suffice to display the natural dignity and unsentiment of wild animals in their cosmos?

When Dr Darling writes that "the aim of science should certainly be to remove the

mystery from natural phenomena, but not to take away wonder or that quality of nature which allows for the development and play of aesthetic appreciation", he is stating a very valuable truth. One feels that most ecologists, and nearly all zoologists, have lost this power of wonder, in their effort to tear away the mystery. CHARLES ELTON.

SHORT REVIEWS

Forest Bibliography to 31*st December*, 1933. *Part I. A. General forestry* (*by countries*). *B. Silviculture.* (1936, pp. 1–78. Price 5*s.*) *Part II. Silviculture* (*continued*). (1937, pp. 79–199. Price 12*s.* 6*d.*) *Part III. Forest protection.* (1938, pp. 200–74. Price 12*s.* 6*d.*) Compiled and published by the Department of Forestry, Oxford University. Obtainable from the Librarian, Department of Forestry, Oxford.

This useful series of bibliographies contains titles of most of the relevant publications in the English language, and a large number in French and German. (It does not cover other languages except where such publications have summaries in English, French or German.) Animal ecologists will find their chief interest in Part III, which is classified under the following sub-headings: Man, Animals (including bird and game preservation), Atmospheric influences, Fire, Weeds, Other agencies (various catastrophes, reclamation, etc.) and Fencing (including hedges). The number of reports dealing with damage by deer is interesting. One disadvantage of the bibliography is that, although the full titles and the abbreviated references are given, the authors' names are given without initials. However, the list will be found very useful by animal ecologists.

Forestry Abstracts. Vol. 1, No. 1, pp. 1–59. Imperial Forestry Bureau, Oxford, 1939. To be issued in four quarterly numbers; subscription direct to the Bureau, from residents of the British Commonwealth and Anglo-Egyptian Sudan, £1 p.a.; from other subscribers £1. 5*s.* p.a.

This periodical is the natural outcome of earlier lists of literature issued by the Bureau, and animal ecologists will find several sections of interest to them, e.g. Forest zoology and Forest protection. Besides abstracts, which are up to the usual high standard of the Imperial Agricultural Bureaux, there are short articles summarizing certain subjects. The résumé's of annual reports issued by various organizations are valuable, since such reports are often hard to get hold of. The abstracts are pleasantly got up and printed by the Oxford University Press.

Edmund Sandars (1939). *A butterfly book for the pocket: including all species to be found in the British Isles, with life-sized coloured plates, and life histories.* 332 small pages, many coloured plates and text figures. Oxford University Press, Amen House, Warwick Square, London, E.C. 4. Price 7*s.* 6*d.*

Those who have already used *A bird book for the pocket* and *A beast book for the pocket* will welcome another of these highly intelligent compilations by Mr Sandars, who refuses to be taken in by the protective jargon of specialists, and yet at the same time keeps a careful standard of accuracy. The present volume on butterflies makes the subject attractive and should enable observers not only to identify the species he meets, but to acquire the wide range of knowledge of their habits and habitats and seasonal cycles which identification makes possible. The author says, in a characteristic introduction: "They neither sting, bite

nor stink. Their capture is difficult enough to amuse, provides exercise not too violent for young or old, and is restricted to hours suitable for the former." So, teachers should find this book a valuable guide in field observation. There are small maps showing general distribution of species, charts of the annual cycle through the months, and a number of delightful illustrations.

Iceland Papers. Volume 1. *Scientific Results of Cambridge Expeditions to Iceland*, 1932–38. (17 reprints bound under one cover.) Oxford University Press, 1939. Price £1. 1*s.*

The British ecologist, who has very few opportunities of working upon communities that are not more or less drastically interfered with by man or his domestic animals, turns naturally to the nearest accessible parts of the Arctic and Subarctic regions. That is partly why a great deal of ecological survey and analysis has been done by summer expeditions to Greenland, Spitsbergen, Iceland, the Faroes, Lapland, and even Arctic Canada. In recent years Cambridge undergraduate exploring parties have concentrated a great deal on Iceland. Thirty-four men went out between 1932 and 1938 (some of them more than once), and the present volume of 17 reprints represents about half the scientific results. Five other papers are mentioned that were not obtained for the volume, and a further fifteen are in preparation for a second volume. The papers include glaciology, geology, geography, ecology and some taxonomy (spiders, Collembola, Oligochaeta). The ecology mostly concerns vegetation (the central desert, the island of Grímsey) and bird populations (gannets, habitat selection, food, etc.). Further workers in Iceland will find this volume worth its high price. The editor has done well to get so many diverse expeditions to pool their results in one convenient volume.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts are issued free with the *Journal*. They can also be obtained separately in stiff covers, printed on one side of the page to allow them to be cut out for pasting on index cards, by non-subscribers, from the Cambridge University Press, Bentley House, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (at least 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, M. Dunbar, C. Elton, F. C. Evans, B. M. Hobby, M. Mare, Barrington Moore, E. Nelmes, F. T. K. Pentelow, H. N. Southern, H. G. Vevers and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. Ecological surveys and habitat notes	
(*a*) Marine and brackish	394
(*b*) Freshwater	395
(*c*) Land	395
(*d*) Small islands	397
2. General reports and taxonomic studies of use to ecologists	398
3. Animal behaviour and the action of environmental factors	399
4. Parasites	402
5. Food and food habits	404
6. Populations	406
7. Migration, dispersal, and introductions	409
8. Reports of organizations	412

1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(a) Marine and brackish

See also **252, 338, 343**

189. Daniel, R. J. (1938). "Report for 1938, Marine Biological Station at Port Erin, Isle of Man." 51: 1–36. University Press of Liverpool. Price 1*s.* 6*d.*

Oyster breeding experiments show that pure cultures of some species of small flagellates form better larval food than others. A list of additions to H. B. Moore's *Marine Fauna of the Isle of Man* contains species new to the area and further distributional and breeding records. An unusual Bryozoan larva is described.

190. Howes, N. H. (1939). "The ecology of a saline lagoon in south-east Essex." J. Linn. Soc. (Zool.), 40: 383–445.

The lagoon was formed by damming a creek of the river Roach nine years before survey took place. Chemical data and extensive collections of fauna and flora were made each month, January 1934–April 1935. Salinity was considerably less than that of sea-water and ratios of ions present altered, iron, phosphates and silicates being abundant and nitrates and nitrites occurring in traces only, suggesting that the organic decomposition cycle must be of unusual type. The carbon dioxide content was so low as to form a limiting factor to the production of phytoplankton. The fauna is described with notes on seasonal abundance. Qualitative and quantitative comparison is made with the surrounding marine fauna and that of Widewater Lagoon near the Adur estuary.

191. Moore, H. B. (1939). "The colonization of a new rocky shore at Plymouth." J. Anim. Ecol. 8: 29–38.

A newly made beach of limestone rock was observed for two years, and compared with a nearby old rocky beach. Plants and animals of the old beach are listed, and the colonization of the new beach is described. The process is one of gradual occupation, and conditions appear unsuitable for most species even after two years.

192. Rees, T. K. (1939). "A *Rivularia bullata-Balanus* community." J. Ecol. 27: 62–5.

A remarkable and quite isolated patch of the alga, *Rivularia bullata*, was found growing on the barnacle, *Balanus balanoides*, on rocks at Kennack Sands near The Lizard, Cornwall. This alga, occurring only sporadically elsewhere, is here the dominant plant, and seems to be completely dependent on the barnacle, the shells of which it colonizes when they are 4–6 months old. This observation emphasizes the importance of treating the community as a biotic entity rather than as a plant or animal one.

193. Purchon, R. D. (1937). "Studies on the biology of the Bristol Channel. II. An ecological study of the beach and the dock at Portishead." Proc. Bristol Nat. Soc. 8: 311–29.

The fauna of the beach associations was quite different from that of the dock, the latter being characterized by a number of Lamellibranchs. Analysis of the oxygen tension, salinity, *p*H and temperature of the water showed no difference for the two regions. At the beach the water was considerably more turbid and the wave action stronger. Laboratory experiments on Lamellibranchs showed an unfavourable reaction to turbidity and water motion, and these two factors were considered responsible for the failure of such animals to colonize the beach. Full lists of species included. (Part I of these studies is a general account by **C. M. Yonge** which immediately precedes this paper, pp. 310–11.)

194. Lloyd, A. J. (1938). "Occurrence of burbot in the estuary of the River Severn." Nature, Lond. 142: 1118–9.

Three specimens of *Lota vulgaris* obtained in the spring of 1938 constitute the first modern records of this fish in the West of England.

195. Rees, C. B. (1938). "Distribution of the polychaete *Ophelia cluthensis* McGuire." Nature, Lond., 142: 576–7.

Records of its occurrence in South Wales and Ireland extend its known range.

(*b*) Freshwater

See also **231, 250, 251, 287, 336, 338, 340, 341**

196. Pearce, E. J. (1939). "*Deronectes griseostriatus* De G. and *Hygrobia tarda* Herbst. (Col.) from the same Irish locality." Ent. Mon. Mag. 75: 126.

These two water beetles were found in pools with a stony-gravel bottom which in places is sandy—the nearest approach to the "silt-bottom" of the customary *Hygrobia*-habitat.

197. Pearce, E. J. (1939). "New and additional Haliplid records for Eire and some notes on variation in British specimens of *Haliplus fulvus* F. (Coleopt.)." Ent. Mon. Mag. 75: 32–6.

Useful Irish distribution records.

198. Peters, B. G. (1938). "Habitats of *Limnaea truncatula* in England and Wales during dry seasons." J. Helminth. 16: 213–60.

The incidence of liver fluke is closely correlated with the population fluctuations of *L. truncatula*. The typical habitats of this snail are described in detail and methods of control suggested. The snail is very much more common in wet seasons since suitable habitats are then extended. A provisional map is given of the present distribution of live fluke in England and Wales.

199. Wailes, G. H. (1939). "The plankton of lake Windermere, England." Ann. Mag. Nat. Hist. 3: 401–14.

Samples of plankton were obtained by vertical hauls from 30 m. with a fine-meshed net, taken every two weeks during fifteen months. A list is given of species obtained together with notes on seasonal abundance and points of structual interest.

200. Reid, D. M. (1939). "On the occurrence of *Gammarus duebeni* (Lillj.) (Crustacea, Amphipoda) in Ireland." Proc. R. Irish Acad. B, 45: 207–14.

The common fresh-water species, *Gammarus pulex*, is replaced in the fresh waters of Ireland by a form exactly similar to the brackish-water form, *Gammarus duebeni*. *G. duebeni* is found in waters which vary greatly in their pH value, although no constant structural difference could be associated with variation in pH. Brackish-water forms of *G. duebeni* appear to be unable to breed in fresh water; spermatozoa did not seem to be affected by the change in salinity, but ova failed to develop after formation. The two physiologically distinct types are referred to as *Gammarus duebeni* α (the fresh-water type) and *G. duebeni* β (the brackish-water type).

201. Gardner, D. M. (1939). "A new planarian record for Scotland." Scot. Nat. 37–8.

The freshwater Turbellarian, *Planaria lugubris*, was locally common during 1937 and 1938 in E. Lothian. The worm is described.

(*c*) Land

See also **272, 287, 289, 291, 306, 336, 338**

202. Lack, D. & Venables, L. S. V. (1939). "The habitat distribution of British woodland birds." J. Anim. Ecol. 8: 39–71.

Survey by the British Trust for Ornithology, and observers organized under the Trust, of all British woodland birds in the main types of wood and main geographical regions of Britain. The habitat factors considered are: open as opposed to closed woods, presence or absence of undergrowth (called secondary growth), holes for nesting, tall trees for nesting or for song posts, and water. A comparative index of frequency of birds in different wood types recognizes eleven types: oak and mixed broadleaf, beech, birch, pine, larch, pine with secondary, pine without secondary, oak and beech with secondary, and oak and beech without secondary, Highland pine, and pine plantations. Both mixed broadleaf woods and natural pine are rich in birds, but plantations of both are poor. Eleven species are confined to broad-leaved woods, and five to coniferous. The former are mainly southern species, and the latter northern.

203. Nicholson, E. M. (1938–9). "Report on the lapwing habitat enquiry, 1937." Brit. Birds, 32: 170–91, 207–29, 255–9.

The main aim of the enquiry was to estimate factors governing the distribution of the lapwing (*Vanellus vanellus*) in Great Britain. Results showed a low correlation with geological features. High ground over 1200 ft. is avoided. Forty-five habitats were distinguished of which the commonest were arable land and permanent pasture above alluvial level. The effect of disturbance of breeding sites is hard to estimate, but it is thought that the lapwing suffers little, because of its mobility and of its habit of feeding at any hour of the twenty-four. A certain amount of quantitative data accompanies this work.

204. Temperley, G. W. (1938). "Cliff nesting of the house martin." Vasculum, 24: 127–8.

For some years there has been a considerable colony of house martins nesting on the cliffs on the Northumberland coast.

205. Wilson, G. F. (1939). "Insect pests of rhododendrons: their distribution in Britain." Proc. R. Ent. Soc. Lond. A, 14: 1–5.

The main pests of rhododendrons in Britain are the Tingitid bug *Stephanitis rhododendri*, the Aleurodid *Dialeurodes chittendeni*, Tortricid moths and the weevils *Otiorrhynchus sulcatus* and *O. singularis*. Distribution maps of two species are given and an appeal is made for records of the occurrence of three of the pests.

206. McDonogh, R. S. (1939). "The habitat, distribution and dispersal of the Psychid moth, *Luffia ferchaultella*, in England and Wales." J. Anim. Ecol. 8: 10–28.

This moth is small, 3–4 mm. long, wingless, case-bearing as a larva, and parthenogenetic. It lives on tree trunks where not shaded, and occasionally on stones, and feeds on lichens, especially *Lecanora*. Its range in England is enclosed by the isotherm of 62° F. for July, except where this month has more than 210 hr. sunshine, and it lies below 400 ft. elevation. Dispersal appears to be by wind, possibly up to several miles. It is inactive below 40° F., and positively phototrophic.

207. Wakely, S. (1939). "Some interesting Microlepidoptera." Proc. S. Lond. Ent. Nat. Hist. Soc.: 106–9.

Useful collecting and breeding notes.

208. Fletcher, T. B. (1939). "Plume larvae in May–June." Ent. Rec. 51: 76–7.

Useful habitat notes.

209. Klimesch, J. (1939). "A contribution to our knowledge of the biology of the species of the genus *Bucculatrix*, Zeller (Micro-Lepidoptera)." Proc. S. Lond. Ent. Nat. Hist. Soc.: 101–5.

General life-history. Includes cross-sectional diagrams of larval mines.

210. Niblett, M. (1939). "Notes on food-plants of the larvae of British Trypetidae." Ent. Rec. 51: 69–73.

A long list compiled partly from personal observations, and partly from published records mostly of Continental origin.

211. Yarrow, I. H. H. (1939). "The Aculeate Hymenoptera of a small isolated sand patch in Dorset." Proc. R. Ent. Soc. Lond. A, 14: 15–16.

The total area of the patch was about 28 sq. ft., but the area of available sand was only about 20 sq. ft. A list of 39 species representing 7 families is given.

212. Barnes, H. F. (1939). "Some gall midge species and their host plant range." Ann. Appl. Biol. 26: 318–47.

Dasyneura alpestris attacks certain species of the subgenus *Euarabis* and one other species which may belong to the subgenus *Lomaspora.* Other subgenera are not attacked. The chrysanthemum midge breeds on autumn flowering chrysanthemums, *C. indicum*, *C. rubellum*, *C. indicum* var. *azaleoides* (*C. azaleanum*) and *C.* Korean Apollo. Eggs were laid but no galls were formed on certain other plants of the *Chrysanthemum* genus and other genera. *Dasyneura tetensi* breeds only on black currant, *D. ribicola* on gooseberry only and *D. plicatrix* on *Rubus* spp. *Thomasiniana oculiperda*, *T. theobaldi* and *T. crataegi* are distinct species having a limited host range.

213. Cohen, M. (1938). "The tomato leaf miner and its control." J. Minist. Agric. 45: 460–2.

Includes life history and alternate host plant notes.

214. Collin, J. E. (1939). "On various new or little known British Diptera, including several species bred from the nests of birds and mammals." Ent. Mon. Mag. 75: 134–54.

Records of Phoridae, Anthomyiidae, Helomyzidae, Chloropidae, Ephydridae, Carnidae and Drosophilidae from little studied habitats.

215. Coulson, F. J. (1938). "Remarks upon British Clavicornia." Proc. S. Lond. Ent. Nat. Hist. Soc.: 75–80.

Useful collecting and habitat notes.

216. Walker, J. J. (1939). "Coleoptera in a limited area at Oxford." Ent. Mon. Mag. 75: 9–11.

A selection of the more interesting beetles from fully 300 species observed in an area of 30 acres of meadow and cultivated land.

217. Goodliffe, F. D. (1939). "Acridiidae (Orth.) in Worcestershire, E. Herefordshire and Shropshire, with a note on their ecology in the Malvern Hills." J. Soc. Brit. Ent. 1: 259–60.

Brief notes on habitat.

218. Petherbridge, F. R., Staply, J. H. & Thomas, I. (1938). "The beet eelworm (*Heterodera schachtii*, Schmidt.)." J. Minist. Agric. 45: 226–36.

Includes life history, host plants and methods of how the eelworms are spread.

(*d*) Small islands

See also **243, 260, 327, 329**

219. Lockley, R. M. (1938). "I know an island." 300 pp., 17 maps and diagrams, and 49 photos. George G. Harrap & Co., Ltd., London. Price 10*s*. 6*d*. (Reviewed in J. Anim. Ecol. (1939), 8: 178–9.

Includes notes on Skokholm, Grassholm, Ramsey, Bardsey (Wales); the Blaskets (Ireland); Fair Isle, N. Ronaldshay (Scotland); also Heligoland, the Faeroes and the Westmann Islands.

220. Darling, F. F. (1939). "North Rona: a North Atlantic island." Proc. Roy. Instn. 30: 519–40.

An account of the topography and natural history of North Rona, dealing more especially with the author's research on the biology of the grey seal.

221. Bertram, D. S. (Editor) **(1938).** "The natural history of Canna and Sanday, Inner Hebrides: a report upon the Glasgow University Canna Expeditions, 1936 and 1937." Proc. R. Phys. Soc. Edinb. 23: 1–71.

Records by various workers upon different groups, prefaced by general descriptions of the topography and vegetation. The sections follow the conventional system of species lists with

habitat notes, etc. on most of them. Some attempt is made to refer these notes to the standard survey of vegetation: this is done especially for Hemiptera (W. H. R. Lumsden). There is a study (by A. J. Haddow) of the settledness of beetles under stones, done by counting and marking individually with paint the larger Carabids. The survey represents a considerable advance, both in completeness and the attention given to ecological data during collecting; but the results are not grouped ecologically so as to give a coordinated picture of the distribution of animal associations, or of their relation to plant associations. There is a good deal of data also for Sanday, Rhum and Òigh-sgeir.

222. Carrick, R. & Waterston, C. (1939). "The birds of Canna." Scot. Nat. 5–22.

Includes a list with distribution and habitat notes of 128 species definitely recorded from Canna since 1881, 47 of which breed there regularly. Since 1890 six species have decreased in number and a few have increased; introduced game birds have not become established. The vegetation has undergone little change which would influence the bird population.

223. Harrison, J. W. Heslop (1939). "Further contributions to our knowledge of the Lepidoptera of the Western Isles of Scotland. I. The Outer Hebrides." Entomologist, 72: 105–9.

A list of 83 species of moths.

224. Harrison, J. W. Heslop (1939). "The gall-making Hymenoptera of some of the Western Islands of Scotland." Ent. Mon. Mag. 75: 60–3.

Part of the survey of the Inner and Outer Hebrides organized by the Department of Botany, King's College, University of Durham.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

225. Scott, T. C. S. Morrison- (1939). "A key to the British bats." Naturalist, 33–6.

A valuable key and summary of distribution and field characters.

226. Scott, T. C. S. Morrison (1934). "Measuring mammals' tails." Ann. Mag. Nat. Hist. 3: 216–19.

Suggests that tail length be measured from the anus rather than from the angle obtained when the tail is bent up at right angles to the body as previously advocated. The exact method of laying out the animal for the new type of measurement is described and such anus measurements are found to be more constant than, and to fall within the extremities of, the old measurements.

227. Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1938). "The handbook of British birds. Vol. 2 (Warblers to owls). Pp. 1–352. (1939.) Ibid. "Vol. 3 (Hawks to ducks)." Pp. 1–387. Both volumes fully illustrated in colour and with text-figures. H. F. & G. Witherby, Ltd., 326 High Holborn, London, W.C. 1. Price £1. 1*s*. per vol. for subscribers to all five volumes; £1. 5*s*. for single volumes.

228. Parker, E. (1939). "Predatory birds of Great Britain." Brit. Field Sports Soc. Publication No. 37. 84 small pp., black and white illustrations. (London, British Field Sports Society, 3 St James's Square, S.W. 1. Price 2*s*.)

A handy book of small size devoting about a page to each species. Local names are given, followed by measurements and brief description, chiefly applicable if the bird is at close quarters, very short notes on the range (sometimes inaccurate, e.g. peregrine) and generalized remarks on food. There is a section giving general conclusions about gulls partly by "a well-known naturalist, whose word carries authority". The conclusion is that "all our gulls with the exception of the kittiwake are harmful in a greater or less degree", a statement which is general enough to be difficult to disagree with. The last 30 pages give the legal periods of protection for each species in each county.

229. Mellanby, H. (1938). "Animal life in fresh water: a guide to British freshwater invertebrates." 296 pp., 211 text-figs. London: Methuen & Co., Ltd. Price 8*s.* 6*d.* (Reviewed in J. Anim. Ecol. (1939), 8: 179.)

230. Browne, F. Balfour- (1938). "Systematic notes upon British aquatic Coleoptera. Being a corrected and revised edition of a series of papers which appeared in the 'Entomologists' Monthly Magazine' from 1934 to 1936. Vol. 1. Hydradephaga." London: Nathaniel Lloyd & Co., Ltd. Price 3*s.* 6*d.*

A systematic work containing many advances upon the standard text-books.

231. Marshall, J. F. (1938). "The British mosquitoes." London: British Museum (Natural History). Price £1.

An exhaustive and well-illustrated monograph with descriptions and keys to adults, larvae and pupae and notes on life-history, ecology, etc. Includes sections on feeding, oviposition, mosquito "control", flight range, rarity, parasitism and malaria in Britain.

232. Mosely, M. E. (1939). "The British caddis flies (Trichoptera). A collectors' handbook." London: George Routledge & Sons, Ltd. Price 21*s.*

The first complete work on the group in English since McLachlan's revision of the European Fauna (1874–84). Contains concise descriptions, keys, figures of wings and genitalia, but few distributional records.

233. Harrison, J. W. Heslop (1939). "The dragonflies of Northumberland and Durham." Vasculum, 25: 40–1.

Includes many distributional records omitted from the standard text-books.

234. Macan, T. T. (1939). "A key to the British species of Corixidae (Hemiptera Heteroptera) with notes on their ecology." Sci. Publ. Freshw. Biol. Ass. Brit. Emp. 1: 1–27. Price (to non-members) 1*s.* 6*d.* (Address: Wray Castle, Ambleside, Westmorland.)

The first of a series of illustrated pamphlets containing keys and references for identifying the lesser-known groups of British freshwater animals.

235. Bagnall, R. S. (1939). "Notes on British Collembola." Ent. Mon. Mag. 75: 21–8, 56–9, 91–102.

The third and fourth contributions of the series, introduces numerous species new to Britain and describes several new to science.

236. China, W. E. (1939). "Additions to the British Homoptera." Ent. Mon. Mag. 75: 41–56.

Important additions to the British list, with descriptions, figures and keys.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **190, 193, 200, 203, 241, 281, 290, 292, 293, 309, 311, 316–17, 320, 338, 340.**

237. Baker, J. R. (1938). "The relation between latitude and breeding seasons in birds." Proc. Zool. Soc. Lond. A, 108: 557–82. (Reviewed in J. Anim. Ecol. (1939), 8: 173–5.)

A generalized study of the breeding seasons of 254 species of birds shows the following scheme; in the tropics the height of the egg season follows roughly the path of the overhead sun, or is slightly before it. This means that to nearly 40° north and south of the equator there are two main peaks in the breeding season, occurring about February and August. Northwards the first of these is accentuated, southwards the second one. Many birds in the equatorial regions do actually breed twice a year, but the majority follow either one or the other of the seasons. There are other compli-

cations: in some orders of birds, e.g. Charadriiformes, Grallae, Herodiones, the breeding season gets earlier, from the boreal region southwards, but from the temperate region southwards it gets earlier again, so that its incidence in the tropics is just in front of the southward sweep of the sun. In the Accipitres, Coraciiformes and Passeres from the temperate zone southwards the breeding season continues to become earlier so that in the tropics it is just in front of the northward sweep of the sun. Generally speaking, little breeding takes place when days are less than 12 hr. in length, and almost none when they are less than 11 hr. However, there is no positive correlation with increasing day length, nor with particularly fast increase of day length. The significant coincidence of tropical breeding with the path of the overhead sun may indicate that light is a proximate cause of breeding, though the incidence of rainy seasons must also have an effect. In the temperate regions temperature and day length may be more important.

238. **Smith, C. Horton- (1938).** "The flight of birds." 182 pp., 17 plates and 30 text-figs. H. F. & G. Witherby, Ltd., London. Price 7*s.* 6*d.* (Reviewed in J. Anim. Ecol. (1939), 8: 178.)

239. **Temperley, G. W. (1939).** "Ornithological report for Northumberland and Durham for the year 1938." Vasculum, 25: 42–51.

Classified notes and discussion of weather and its effect on bird movements.

240. **Lovern, J. A. (1939).** "Captive eels: some observations on their behaviour." Salm. Trout Mag. No. 94: 56–7.

Notes on feeding and behaviour of eels in fresh and salt water.

241. **Petherbridge, F. R. & Wright, D. W. (1938).** "The cabbage aphis (*Brevicoryne brassicae* L.)." J. Minist. Agric. 45: 140–8.

Life history. The distance travelled by the winged forms appears to be considerable, several miles. Natural rate of increase is chiefly governed by climatic factors. Dry, warm conditions are very favourable for increase and the production and migration of winged forms. Cool, wet weather and especially heavy rainstorms reduce the numbers. Among the biological agencies are chiefly insect predators and secondarily insect parasites. Hover flies and gall midge larvae are among the more important predators.

242. **Worms, C. G. M. de (1939).** "Insects at light." Proc. S. Lond. Ent. Nat. Hist. Soc.: 80–4.

Includes brief descriptions of traps and discussion of main problems involved. See also **L. H. Ennis**, Proc. S. Lond. Ent. Nat. Hist. Soc.: 85–8.

243. **Harrison, J. W. Heslop (1939).** "The fate of pupae resulting from the Outer Hebridean *Pieris brassicae* immigrants of 1937." Entomologist, 72: 93.

Suggests that delayed emergence may account for erratic appearances of this butterfly in the Hebrides.

244. **Edelsten, H. M. (1939).** "*Lycaena dispar batavus* Obr. at Wood Walton Fen, 1938 (Lepid.)." Proc. R. Soc. Lond. A, 14: 6.

The colonies of the Dutch race of this butterfly, recently introduced into Wood Walton and Wicken Fens to replace the extinct British race, suffered rather heavily this spring owing to the inclement weather. The late frosts cut down the young dock leaves just as the larvae had emerged from hibernation, and ensuing drought delayed the growth of fresh leaves. The larvae consequently were short of food and it is believed some died of starvation. The insect appears to have remarkable powers of resistance and in spite of the adverse conditions sufficient butterflies emerged to produce a good stock of larvae.

245. **Whitney, R. J. (1939).** "The thermal resistance of mayfly nymphs from ponds and streams." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 44–8.

The thermal resistance of six species of Ephemerid larvae (*Baëtis rhodani*, *B. tenax*, *Rhithrogena semicolorata*, *Ecdyonurus venosus*, *Caenis* sp. and *Cloeon dipterum*) was measured by finding the temperature at which 50% were killed in 24 hr. Species exposed in nature to higher or more variable temperatures were more resistant than others.

246. Callan, E. McC. (1939). "Notes on the woodwasp, *Xiphydria dromedarius* F., on the cricket-bat willow." J. Soc. Brit. Ent. 1: 242–4.

The woodwasp, *Xiphydria dromedarius*, which appears to be more common than is generally supposed, was found on a number of occasions on or near the cricket-bat willow, *Salix alba* var. *caerulea*. Woodwasps were observed ovipositing in the trunk of a young bat willow recently killed by the honey fungus, *Armillaria mellea*, under circumstances such as to suggest that trees which are still green, but in which the wood is drying, are attractive for oviposition, while living trees are unsuitable.

247. Thorpe, W. H. & Caudle, H. B. (1938). "A study of the olfactory responses of insect parasites to the food plant of their host." Parasitology, 30: 523–8.

In the case of *Pimpla ruficollis*, a parasite of the pine shoot moth *Rhyacionia buoliana*, it has been shown that the parasites are only attracted by the oil of *Pinus sylvestris* when they are 3 or 4 weeks old, at which time the gonads become mature. Apparently the parasite finds the food plant of its host by a positive olfactory response which only develops when the eggs are ready for laying.

248. Callan, E. McC. (1939). "Assembling of *Thersilochus rufiventris* Brisch. (Hym., Ichneumonidae)." J. Soc. Brit. Ent. 1: 244–5.

Some hundreds of assembling males in a peculiar dancing flight around females ovipositing in the galls of the willow saw-fly.

249. MacLeod, J. (1939). "The seasonal and annual incidence of the sheep tick, *Ixodes ricinus*, in Britain." Bull. Ent. Res. 30: 103–18.

Tick incidence is greatest in spring and decreases markedly in early summer. Seasonal activity was found to be related to the air temperature, expressed as the weekly average of maximum temperatures. The limits of the air-temperature range corresponding to active tick infestation are 45 and 60° F.

250. Moon, H. P. (1939). "Aspects of the ecology of aquatic insects." Trans. Soc. Brit. Ent. 6: 39–49.

Stresses difficulty in correlating collecting results with physico-chemical factors. Shows how *p*H controls the arrangement of the fauna over a very large area, but is inadequate to explain details. Brings forward evidence that the substratum is the important factor in distribution. In lakes and streams, as the habitat evolves, there is gradual replacement of the food chains dependent on algae by those dependent on silt and detritus. The fauna is to a very large extent controlled by amount of erosion or deposition taking place. Silt may be used as an indicator of the intensity at which these processes are taking place and as a standard of comparison of diverse habitats.

251. Moon, H. P. (1939). "Importance of the substratum to the invertebrate animals on which fish feed." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 36–40.

A general discussion, with examples from the Avon and its tributaries, of the influence of the nature of the river bed on the distribution of the fauna.

252. Gillam, A. E., El Ridi, M. S. & Wimpenny, R. S. (1939). "The seasonal variation in biological composition of certain plankton samples from the North Sea in relation to their content of Vitamin A, carotenoids, chlorophyll, and total fatty matter." J. Exp. Biol. 16: 71–88.

Parallel chemical and biological studies of the plankton of the southern North Sea. The total plankton depends on three diatom outbursts, in May, August and October. Carotene, chlorophyll and vitamin A were detected in the gross plankton extracts, fucoxanthin only in few cases. The seasonal variation of chlorophyll most nearly coincided with the total mass of the plankton; carotenoids reached their peak slightly before the maximum biological development, while vitamin A content reached its maximum in the month after the spring diatom outburst.

253. Hawes, R. S. (1939). "The flood factor in the ecology of caves." J. Anim. Ecol. 8: 1–5.

Floods introduce a variable into the otherwise constant environment of caves. They bring about an annual rhythm in the life cycle of certain cave-dwelling animals. They introduce food into caves and they may cause the initial colonization of caves by fish originally living in above-ground waters. The discussion is based on observations in Jugo-Slavia.

254. Callendar, G. S. (1939). "Some interesting temperature anomalies for 1938." Quart. J. R. Met. Soc. 65: 137.

In most North Atlantic countries the mean temperature of last year was remarkably high and at several stations in North America, Scotland, and the Baltic countries it equalled or exceeded previous record values.

255. Keen, B. A. (1939). "What happens to the rain?" Quart. J. R. Met. Soc. 65: 123–37.

It is only in recent years that a true picture of the movement of water in the soil has been built up. In consequence, some of the traditional practices need revision, while others now have a different explanation. The new work has also clarified some of the concepts used in hydrology.

256. Manley G. (1939). "On the occurrence of snow-cover in Great Britain." Quart. J. R. Met. Soc. 65: 2–27.

Hitherto practically no information has been forthcoming with regard to the frequency with which a snow-cover may be expected on the uplands and mountains of Great Britain. Variations with altitude from year to year are very great. A relationship has now been derived between the mean temperature of the winter months and the average frequency of occurrence of snow-lying, which after test appears to be generally applicable to any given place over a period of years. It is necessary, however, to allow for several additional factors, notably quantity of snowfall, which influence the duration of snow-cover. It appears that, making these allowances, a reasonable estimate can be made of the frequency of snow-cover at the majority of places in Great Britain; also, of the extent to which the expectation of snow-cover varies with small fluctuations in mean winter temperature over a period.

257. Day, W. R. (1939). "Local climate and the growth of trees with special reference to frost." Quart. J. R. Met. Soc. 65: 195–209.

The type of forest is largely determined by the general climate, but local climatic conditions exercise considerable influence. The natural forest in this country is composed of species, some of which are relatively hardy to frost, whereas others are, in comparison, easily injured by it. The latter species usually form the final woodland, and their successful growth is made possible by the development of favourable conditions of climate and soil within woodland formed first of all by hardy species. Examples are given to illustrate the effect of overhead and side shelter on the temperature of the air over the ground. The influence of topography on frost is also illustrated and discussed. The effect of accessory factors, such as soil fertility, local warm or cold situations, and the general suitability of the exotic species to the climate to which they are introduced are also shortly discussed in relation to the occurrence of frost injury.

4. PARASITES

See also **198, 247, 248, 249, 309, 332**

258. Thompson, G. B. (1939). "A check-list and host-list of the ecto-parasites recorded from British birds and mammals. Part I. Mammals (excluding bats)." Trans. Soc. Brit. Ent. 6: 1–22.

Includes references and notes on comparative abundance. Gives special attention to parasites of the various island forms.

259. Thompson, G. B. (1939). "A list of the type-hosts of the Mallophaga and the lice described from them." Ann. Mag. Nat. Hist. 3: 241–52.

A further instalment of a list of bird hosts of lice and of the species which prey upon them.

260. Carrick, R. (1939). "Some parasites of birds and mammals from Canna." Scot. Nat.: 23–4.

Lists, with brief notes, of endoparasites (1 trematode, 1 cestode, 2 nematodes) taken from a sheep, and ectoparasites (4 Mallophaga, 4 Siphonaptera) taken from a rabbit, a dog, a pigmy shrew, pigs, starling, shag, nest of kittiwake and hen-houses on the Isle of Canna during July, 1936. One of the nematodes, *Bunostomum trigonocephalum,* was found also in a rabbit.

261. O'Mahony, E. (1939). "A preliminary list of Irish fleas." Ent. Mon. Mag. 75: 124–6.

List of 20 species with records of hosts.

262. Hopkins, G. H. E. (1939). "Straggling in the Mallophaga." Entomologist, 72: 75–7.

In most cases a given species of bird-louse has only one true host, though it may be found accidentally on unrelated hosts and more or less normally on closely-related species. As knowledge of systematics increases, the number of instances in which a given species is found to occur normally on more than one species of host is being reduced. When a species is found to be common to two hosts, a much closer relationship between them is required than was formerly thought to be the case. The dangers of accidental straggling due to imperfections in technique after the host has been shot, and casual straggling, e.g. in zoological gardens, are discussed; also normal straggling among sea-birds and water-fowl breeding or feeding in company, and true polyoecism.

263. Stunkard, H. W. (1938). "The development of *Moniezia expansa* in the intermediate host." Parasitology, 30: 491–501.

This Anocephaline Cestode, the adult of which infects rabbits, is found to develop to the cysticercoid phase when the eggs are fed to Galumnid mites. It is suggested that mites serve as intermediate hosts for *Moniezia* and probably for other Cestodes of this group.

264. McDonogh, R. S. (1939). "The parasites of *Luffia ferchaultella* (Stephens) (Lepidoptera, Psychidae)." Proc. R. Soc. Lond. A, 14: 41–6.

The larvae of this moth are not very highly parasitized, probably owing to the protection afforded by the larval case; but 13 species of 6 genera of Ichneumonidae, 6 species of 6 genera of Chalcididae, 2 genera of Braconidae, and 1 species of Proctotrupid were bred during the two summers of 1935 and 1936. A fairly large proportion of the species belonged to genera normally hyperparasitic, but it appears likely that they were not so in these cases.

265. Brindley, M. D. (1939). "Observations on the life-history of *Euphorus pallipes* (Curtis) (Hym.: Braconidae), a parasite of Hemiptera-Heteroptera." Proc. R. Ent. Soc. Lond. A, 14: 51–6.

It is well known that some Homoptera, notably the Aphididae, are extensively parasitized by Hymenoptera. The Heteroptera are apparently less subject to this kind of attack, but in recent years, in different parts of the world, certain Braconidae have been reared from Pentatomid or Capsid bugs. These parasites all belong to the subfamily Euphorinae which has a wide geographical distribution. It is still undetermined how far this group of Braconidae is specific for different bugs.

266. Andrews, H. W. (1939). "The family Cyrtidae (Diptera)." Proc. S. Lond. Ent. Nat. Hist. Soc.: 76–9.

A compilation not embodying original work, but bringing together a number of facts concerning their life-history etc. from scattered sources. The larvae are parasitic on spiders.

267. Goodliffe, F. D. (1939). "A joint infestation of Barley by *Lasiosina cinctipes* Mg., together with *Chlorops taeniopus* Mg. (Diptera, Chloropidae) and their Hymenopterous parasites." J. Soc. Brit. Ent. 1: 248–52.

25% of the shoots failed to produce normal ears, more than one-third of the Chloropid larvae were parasitized by a Chalcidid and 16% by a Braconid.

268. Hanson, H. S. (1939). "Ecological notes on the *Sirex* wood wasps and their parasites." Bull. Ent. Res. 30: 27–76.

A single generation of *Sirex* can support three generations of *Rhyssa* and one generation of *Ibalia*. Effects of parasitism by *Rhyssa* are cumulative. Superparasitism of *Ibalia* by *Rhyssa* is very frequent. Both parasites are efficient, but the combined effects of the two parasites result in a higher percentage of parasitism than when each is working alone. Parasitism by *Rhyssa* is highest when the *Sirex* is breeding in material under 3 in. in diameter, thus within reach of the *Rhyssa* ovipositor. The effective activity of *Ibalia* is limited to the egg and early larval stage of the host. Other factors in *Sirex* control are discussed, e.g. birds, fungi and climatic control.

269. Wilkinson, D. S. (1939). "On the identity of *Apanteles infimus* Haliday and of *Apanteles infimus* Haliday of Marshall (Hym. Bracon.)." Proc. R. Ent. Soc. Lond. B, 8: 53–60.

Includes distributional and host records.

270. Harrison, J. W. Heslop (1939). "A Dipterous parasite on the mollusc *Cochlicella barbara* on the Islands of Barra, South Uist and Canna." Entomologist, 72: 99.

A heavy percentage of the catch was parasitized by Dipterous larvae which emerged by boring a round hole in the shell and pupated in November and December. The adult has not been bred and the species is as yet undetermined.

271. Callan, E. McC. (1939). "*Cryptorrhynchus lapathi* L. in relation to the watermark disease of the cricket-bat willow." Ann. Appl. Biol. 26: 135–7.

Although this beetle has transmitted *Pseudomonas saliciperda*, the agent causing a watermark disease of willows in Holland, negative results were obtained in attempts to get this beetle to transmit *Bacterium salicis* the cause of watermark disease of cricket-bat willow in this country.

5. FOOD AND FOOD HABITS

See also **189, 241, 252, 253, 283, 305, 334**

272. Turner, J. S. & Watt, A. S. (1939). "The oakwoods (*Quercetum sessiliflorae*) of Killarney, Ireland." J. Ecol. 27: 202–33.

Deer, both the red (*Cervus elaphus*) and the Sika or Japanese (*Cervus nippon*) are very frequent around the lake. They remove the bark from the holly and graze the shoots. In winter they live mostly in the valley woods, where holly is often lopped to provide them with food. They are poached by burning *Molinia* pasture to attract them to the young grass where they are shot.

273. Thomas, J. F. (1938). "Food of nestling swallows." Brit. Birds, 32: 233–6.

Table of insects taken from adult swallows (*Hirundo rustica*) as they came to the nest to feed the young. The observations were conducted from mid-June to the end of August. Diptera were the commonest prey. It is recorded that one bird returned with 31 flies.

274. Thomas, J. F. (1939). "The food of the Little Owl. Derived from pellets, February 1936 to January 1937. Results of a year's observations of a single bird, its mate and family (South Downs, Seaford)." Discovery, 2: 94–9.

A detailed report on 368 pellets; among other prey includes records of 6 birds, 50 rodents, 1325 ground beetles, 1023 Staphylinid beetles and 5232 earwigs.

275. Eve, F. C. (1939). "Stomach pump for trout: a new substitute for autopsy." Salm. Trout Mag. No. 94: 33–7.

A useful method of obtaining stomach contents without killing the fish.

276. Soong, M. K. (1939). "Preliminary notes on the food of young trout and salmon parr." Avon Biol. Res. Ann. Rep. No. 6, 1937–8: 34–5.

137 trout and 17 salmon were examined, all from the same pool. Differences in the food of the two species were noted.

277. Carpenter, K. E. (1939). "Food of salmon parr." Nature, Lond., 143: 336.

Feeding is totally indiscriminate, but food organisms of sub-aerial origin are more numerous in the stomachs than aquatic types, and the number of Hemipteran plant pests suggests the desirability of encouraging the growth of trees and shrubs along the banks of streams.

278. Allen, K. R. (1939). "A note on the food of pike (*Esox lucius*) in Windermere." J. Anim. Ecol. 8: 72–5.

Pike over 30 cm. long fed almost entirely on other fish, principally perch (42% of those examined) and very little on trout (only 2%). A high percentage had empty stomachs.

279. Evans, A. C. (1938). "Physiological relationships between insects and their host plants. 1. The effect of the chemical composition of the plant on reproduction and production of winged forms in *Brevicoryne brassicae* L. (Aphididae)." Ann. Appl. Biol. 25: 558–71.

Under late summer conditions of light, the rate of reproduction is positively correlated with the nitrogen content of the host plant and, in particular, the protein content. The formation of winged forms is negatively correlated with the same factors. The chemical composition of the plant affects the amount of food eaten, the rate of growth, length of larval period and final pupal weight of *Pieris brassicae*.

280. Harrison, J. W. Heslop (1939). "The food-plants of *Pieris napi* in the Inner and Outer Hebrides." Entomologist, 72: 79–80.

Owing to the erratic distribution of possible food-plants, these differ from station to station, and even to some extent from isle to isle.

281. Evans, A. C. (1939). "The utilization of food by certain Lepidopterous larvae." Trans. R. Ent. Soc. Lond. 89: 13–22.

The food relationships of the larvae of *Phalera bucephala*, *Aglais urticae*, *Smerinthus populi*, *Malacosoma neustria* and *Pieris brassicae* have been studied. The coefficient of utilization of food falls steadily during the 1st and 2nd instar of *P. bucephala*; during the 3rd, 4th and 5th instars it fluctuates irregularly. The consumption, utilization and metabolism of food per gram of larva per day follow a similar course. The coefficient of growth increases until the middle of the 3rd instar and then fluctuates irregularly. About 90% of the water contained in the food is extracted during the first four days of larval life. The larvae of the species studied utilize and consume food at very different rates. The amounts of carbohydrate, fat and ash utilized per gram of larva per day differ very much in the four species. The nutritive ratio of the larvae is very much lower than that of certain growing mammals, i.e., cattle, sheep and pigs, and the difference seems to be correlated with the chemical composition of the tissues.

282. Blair, K. G. (1938). "Midges attacking other insects." Proc. S. Lond. Ent. Nat. Hist. Soc.: 84–5.

Includes survey of all known records. Though such records are as yet too few for certainty, they at least afford indications that each genus or species of midge that acquires this habit limits its victims to a particular order of insects.

283. Wilson, F. (1938). "Notes on the insect enemies of *Chermes* with particular reference to *Pineus pini*, Koch, and *P. strobi*, Hartig." Bull. Ent. Res. 29: 373–89.

No parasites of this scale-insect were found. The predators fall into three groups: (*a*) those which remove the wool from the *Chermes* before feeding, (*b*) those which enter the wool mass and attack the *Chermes* from within, and (*c*) those which do not enter the wool mass but attack the *Chermes* from outside. The major predators are *Leucopis obscura* (Ochthiphilidae), *Lestodiplosis pini* (Cecidomyidae), *Hemerobius stigma* (Hemerobiidae), *Wesmaelius concinnus* (Hemerobiidae) and *Exochomus quadripustulatus* (Coccinellidae).

284. Yarrow, I. H. H. (1939). "Observations on *Asilus crabroniformis* (L.) (Diptera)." Proc. R. Ent. Soc. Lond. A, 14: 17.

A female robber-fly was kept under observation for about an hour, during which time it made nineteen attempts upon passing insects, eventually securing the Staphylinid beetle *Philonthus aeneus*.

285. Hobson, R. P. (1938). "Sheep blow-fly investigations. VII. Observations on the development of eggs and oviposition in the sheep blow-fly, *Lucilia sericata* Mg." Ann. Appl. Biol. 25: 573–82.

Two meat meals are necessary for the development of mature eggs in the ovaries and neither plant materials nor animal excreta can replace the meat in the diet of the female.

286. Johnson, C. G. & Mellanby, K. (1939). "Bed-bugs and cockroaches." Proc. R. Ent. Soc. Lond. A, 14: 50.

It is widely believed that cockroaches eat bed-bugs and that some measure of control of *Cimex* may thus be affected, but experiments show that this is unlikely.

287. Reynoldson, T. B. (1939). "Enchytraeid worms and the bacterial bed method of sewage treatment." Ann. Appl. Biol. 26: 138–64.

The flora and fauna of a bacterial bed is discussed, a definite cycle of *Phormidium* being described. The worms feed primarily on *Phormidium* and are important agents in the spring off-loading of this alga. There is no summer off-loading owing to increased temperature and sunlight which lessens the effect of the worm depredations.

6. POPULATIONS

See also **2, 199, 203, 211, 220, 222, 244, 249, 252, 268, 318, 334, 337, 338, 339, 340, 341, 342**

288. Matheson, C. (1939). "A survey of the status of *Rattus rattus* and its subspecies in the seaports of Great Britain and Ireland." J. Anim. Ecol. 8: 76–93.

Intensification of efforts to eradicate rats (almost all black rats) on board ships has succeeded in reducing the number of ships requiring fumigation, and the number of rats per ship fumigated. Nevertheless, the undiminished black rat population on shore at several ports, and simultaneous decrease of brown and black rats at other ports, indicate that the black rat can maintain itself on shore without additions from the ships.

289. Taylor, W. L. (1939). "The distribution of wild deer in England and Wales." J. Anim. Ecol. 8: 6–9.

The population of wild deer is larger than generally recognized, and is increasing. Besides the two native species, the red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), of which the former is numerous in West Somerset and Devon, there is the fallow deer (*Dama dama*) of uncertain status, also three introduced species, the Japanese (*Sika nippon*), the Chinese muntjac or barking deer (*Muntiacus reevesi*), and the Siberian roe (*Capreolus pygargus*), which have escaped and are tending to increase their range and numbers. Where plentiful, deer cause losses to farms and woodlands. A list compiled from the notes of Forestry Commission officers gives the species and estimated relative local abundance in each county.

290. Warwick, T. (1939). "Some habits of pipistrelle colonies." Scot. Nat. 68–70.

Well established colonies of *Pipistrellus pipistrellus* in the rafters, etc., of cottages in the Tweed Valley, Selkirkshire, where they are very abundant, were under observation during July 1937, and May and June 1938. Large and small colonies may live under the same roof and still retain their individuality. Sounds of activity can be heard in the evening for about an hour before the bats emerge in a succession of small parties. In dull weather emergence is later, the parties are smaller and less time is spent on the wing. There is marked sexual segregation of adults during pregnancy and in May and June the main colonies of males were not located. Immature individuals of both sexes were sometimes found during those months with the females, but adult males did not join them till mid-July. A list of four other British species showing sexual segregation in summer is given.

291. Lister, M. D. (1939). "An account of the lapwing population of a Surrey farm." Brit. Birds, 32: 260–71.

Fluctuations in numbers of a particular area were studied over five years. Larger numbers were recorded during the last three years, which may be due to increase of grassland in the area. The first peak usually occurred in September and then fluctuations were erratic until January or February, when they declined to the normal breeding population. Flocks frequented grassland mostly, but would often move in numbers to arable land, especially when newly ploughed or after rain.

292. Southern, H. N. (1939). "The flocking of immature herons." Brit. Birds, 32: 346–9.

Flocking at a locality in Hertfordshire 8 miles from the nearest heronry occurred from spring to early winter, numbers rising to a peak from July to September. Practically all birds were immature.

293. Lack, D. (1939). "The display of the blackcock. I. Mid-April observations." Brit. Birds, 32: 290–303.

The "lekking" of the blackcock (*Lyrurus tetrix*) is described. Each male defends a special area of its own from which any other bird, however strong, will retreat, if attacked. This may reduce disturbance during copulation. An apparently pointless recrudescence of this display occurs in autumn.

294. Fisher, J. (1939). "The history of the Irish gannet colonies." Brit. Birds, 32: 314–19.

295. Marchant, S. (1939). "The Irish gannet colonies, 1938." Brit. Birds, 32: 320–5.

Census figures for Little Skellig and Bull Rock.

296. Southern, H. N. (1938). "Distribution of the bridled form of the common guillemot (*Uria aalge*)." Nature, Lond., 142: 951–2.

Field counts of the proportion of different varieties of the common guillemot in colonies of the British Isles indicate increasing percentages of the bridled form as one goes from south to north. English and Welsh colonies have less than 1%, 10–13% is characteristic of north Scotland, and 24% is recorded for Shetland. This cline is continued northward and southward of the British Isles. There appears to be another cline in *U. aalge* in the amount of melanin pigmentation on the back, northern birds being considerably darker than those in the southern part of the range.

297. Chislett, R. (1939). "The black-headed gull (*Larus ridibundus*) in Yorkshire." Naturalist: 125–30.

A detailed account of a survey of breeding colonies of the black-headed gull in Yorkshire, undertaken as part of the British Trust for Ornithology survey of this species.

298. Graham, M. (1938). "The trawl fisheries: a scientific and national problem." Nature, Lond. 142: 1143–6.

Trawl fisheries have been unprofitable for many years and the number of British fishermen has been considerably reduced since 1919. The relation of natural increases in stocks of fish to the original stocks may be compared to the relation of "principal" and "interest" in finance. Fishing often takes some of the principal as well as the interest, and stocks are then increasingly reduced. An analysis of general statistics of haddock and plaice catches shows that the increase of time and expense of fishing has greatly outweighed the increase in yield, so that much effort has been wasted, and the stock has been reduced to a low level. Estimates of increase of stock based on rates of reproduction, growth and mortality likewise indicate the desirability of a large cut in fishing expenses. The weight of a stock growing in an empty area follows the logistic S-shaped curve which is characteristic of the growth of many populations. As the fishery develops, the rate of fishing increases until the ratio of effort to yield becomes so great as to make further fishing unprofitable. A reduction in the rate of fishing, such as might be effected by limited quotas of each species for each area, is necessary for a satisfactory and economic solution of this problem.

299. Gerrish, C. S. (1939). "Scales of Avon trout and grayling." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 54–62.

Data on age and growth rates of 30 trout and 102 grayling, deduced from scale-readings.

300. Went, A. E. J. (1939). "Salmon in Éire: a study of the runs in 1937 and 1938." Salm. Trout Mag. No. 94: 44–55.

Discusses the salmon shortage in Eire in the last two years. Concludes that in 1937 three (grilse, small spring and summer fish) of the four most important age-groups were deficient and in 1938 all four (including also the large spring fish). In 1938 the fish were poorer in condition (weight/length ratio) than is normal. The only explanation appears to be unknown factors in the sea.

301. Hutton, J. A. (1939). "Wye salmon: results of scale-reading, 1938." Salm. Trout Mag., No. 94: 59–73.

Statistics of the catch, by rods and nets, of salmon in the river Wye. The total catch for the year was 2045 fish weighing 31,985 lb., the worst on record. 648 sets of scales were received for the determination of age. An abnormally high proportion (12·8%) were previously spawned fish. All classes, except the small summer fish, were below the average in condition (weight/length ratio). Hutton believes that the poor catch was due to depletion of the stock by unfavourable conditions of nature unknown in the sea.

302. Nall, G. H. (1939). "Notes on scales from Avon salmon smolts in 1938." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 16–26.

Age-determination from scales of 954 migrating salmon smolts trapped in the Avon in the spring of 1938. Approximately 90% were one year old, 9% two, and 1% three. Many had made rapid growth during the migration season.

303. Berry, J. (1939). "Account of hatching and stocking experiments." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 27–33.

A summary of experiments carried out for five consecutive years (1) to compare natural spawning with the sowing of artificially fertilized eggs of salmon and (2) to compare four methods of stocking with trout (with eyed ova, alevins, unfed fry and fed fry). He concludes that the experiments were on too small a scale to provide the required information, but the details are useful.

304. Lucas, C. E. (1938). "Some aspects of integration in plankton communities." J. Cons. Int. Explor. Mer. 13: 309–22.

A suggestive review of the numerous ways in which the zoo- and phytoplankton may interact. Stress is laid on non-predatory relationships.

305. Wimpenny, R. S. (1938). "Diurnal variation in the feeding and breeding of zooplankton related to the numerical balance of the zoo-phytoplankton community." J. Cons. Int. Explor. Mer. 13: 323–37.

There is a tendency for zooplankton to graze chiefly at night and shed ova by day, while diatoms show a reciprocal time relationship in their assimilation and reproduction.

306. Baweja, K. D. (1939). "Studies of the soil fauna, with special reference to the recolonization of sterilized soil." J. Anim. Ecol. 8: 120–61.

The work deals only with the soil macro-organisms belonging in the field of the entomologist, not with the micro-fauna or other micro-organisms dealt with by the micro-biologist. It was carried on at the Rothamstead Experimental Station from November 1935 to March 1937. Twelve plots of 9 × 9 in., of which four were controls, were arranged in four series to bring out the effect of inclosure with plates set 1 ft. in the ground, and of sterilization in February and in May. Sterilization was by removing the first foot of soil, baking it at 212° F. for 6 hr., and replacing it. The population in the sterilized soils equalled that in the controls in five months in the enclosed and in seven months in the unenclosed plots, and thereafter increased markedly above that of the controls. The insects, except for minor orders, increased beyond their normal numbers, while none of the other invertebrates except Araneida regained their normal density. Recolonization was neither from the sides nor from below, but from above. The possibility of damage to hothouse crops from large increases of injurious insects in sterilized soil is pointed out, and further investigation of soils sterilized by natural heat, as in the tropics, is suggested.

307. Davies, W. M. (1939). "Studies on aphides infesting the potato crop. VII. Report on a survey of the aphis population of potatoes in selected districts of Scotland (25 July–6 August 1936)." Ann. Appl. Biol. 26: 116–34.

Population figures from 43 centres analysed with a view to establishing any relation there might be with (*a*) proximity to winter host plants, and (*b*) meteorological conditions such as temperature, humidity and wind velocity. The results indicate special precautions necessary to ensure health in seed-potato stocks.

308. Harrison, J. W. Heslop (1939). "The recent scarcity of *Plusia iota*, *P. pulchrina* and *P. chrysitis* locally." Vasculum, 25: 31.

Although formerly abundant in Durham and Northumberland these three species of moths are now exceedingly rare.

309. Hardy, J. E. (1938). "*Plutella maculipennis* Curt., its natural and biological control in England." Bull. Ent. Res. 29: 343–72.

Life history, distribution and natural control of this moth, both physical and biotic. *Angita cerophaga* and *A. fenestralis* were the only parasites numerically important, but both apparently overwinter in other hosts. There is a key to the parasites and hyperparasites of *Plutella*. The upper limiting temperature of *Plutella* is approximately 40° C. and the lower for breeding purposes is about 10° C. Rain at certain critical times may be a controlling factor.

310. Blair, K. G. (1938). "Changes in the insect population of Britain during the last 100 years." Proc. S. Lond. Ent. Nat. Hist. Soc.: 61–7.

Deals with Lepidoptera and Coleoptera. The cases fall into two main groups: those species which are strictly local in their habits and which are readily exterminated in any particular locality by the disturbance of the ecological conditions pertaining to such locally, and those with a more general distribution throughout the country.

7. MIGRATION, DISPERSAL AND INTRODUCTIONS

See also **3, 6, 206, 218, 221, 238, 239, 241, 244, 253, 262, 289, 302, 306, 339, 342**

311. Southern, H. N. (1938). "The spring migration of the willow-warbler over Europe." Brit. Birds, 32: 202–6.

The rate of spread of the willow-warbler (*Phylloscopus trochilus*) is shown on a map by isochronal lines at fortnightly intervals. Isotherms of 48° F. are also shown and considerable conformity is noticed, though the birds tend to lag behind the spring at the start and to outstrip it towards the finish. The spread lasts from March 5th (Gibraltar) to June 1st (Inari), and covers 2500 miles in 88 days. It is suggested that the quicker start in this species than in the swallow may be due to the willow-warbler not taking prey on the wing.

312. Ticehurst, N. F. (1939). "The migratory status of the heron in Great Britain." Brit. Birds, 32: 242–6.

Most British herons (*Ardea cinerea*) are stationary, and winter immigrants from Europe are preponderantly immature birds.

313. Skovgaard, P. (1939). "Iceland birds visiting Scotland." Scot. Nat.: 61–7.

A list is given of birds ringed in Iceland during 1921 and recovered in Scotland, with ringing details and dates of recapture. Other countries in which recoveries of each species have been made during this investigation are noted for comparison. Of the 15,000 birds liberated, only a few (13 species) were recovered in Scotland. Migration maps are given for pintail, red-breasted merganser, and meadow pipit.

314. Thomson, A. L. (1939). "The migration of the gannet: results of marking in the British Isles." Brit. Birds, 32: 282–9.

First-year gannets (*Sula bassana*) migrate further south during their first winter than adults.

315. Lockley, R. M. (1939). "The sea-bird as an individual: results of ringing experiments." Nature, Lond., 143: 141–4.

Skokholm Island, on the coast of Pembrokeshire, has been used as a bird observatory station for a number of years. Study of individual birds by ringing has produced much valuable material for life histories. The Manx shearwater, storm petrel and puffin have been shown to have long incubation and fledging periods, followed by an abrupt desertion of the young, which then fast for some days before making their way to the water. Shearwaters winter as far south as the Bay of Biscay, but return in February to occupy their former nesting sites. Pairing appears to be for life, but young birds do not breed until nearly two years old. Birds taken to the Faeroe Islands and to Venice have returned within a very short time to their nests on Skokholm. At the present time, this station is being carried on entirely by voluntary support, but it managed to ring more than 6000 birds in 1938.

316. Parker, H. W. (1939). "Marine turtles as current indicators." Nature, Lond., 143: 121.

The occurrence of seven turtles, four of them identified as common loggerheads, on the British coasts during December 1938 suggests that there has been a strong drift of warm surface water into the English Channel from the south-west.

317. Russell, F. S. (1939). "Turtles in the English Channel." Nature, Lond., 143: 206–7.

The presence of marine turtles in British waters might be associated with an extension of the northern range of these animals and a consequent shifting of the centres of distribution.

318. Smith, E. P. (1939). "On the introduction and distribution of *Rana esculenta* in East Kent." J. Anim. Ecol. 8: 168–70.

Twelve specimens introduced in the winter of 1934–5 increased to large numbers, and, in 3½ years spread over a square of about 28 miles, mostly connected by water. They migrate in June and October, occupying a small pond for a year, abandoning it one or two years, and returning in large numbers. In 1938 their very loud singing suddenly abated, and, though they are still numerous, it is suggested that they are on the way to the semi-extinction of earlier introductions elsewhere in the British Isles.

319. Dahl. K. (1939). "Homing instinct in salmon: the case for separate river races." Salm. Trout Mag. No. 94: 19–26.

A résumé of the evidence for the return of salmon to the rivers in which they were reared.

320. King, G. M., Jones, J. W. & Orton, J. H. (1939). "Behaviour of mature male salmon parr, *Salmo salar* juv. L." Nature, Lond., 143: 162–3.

Groups of mature males taken from the River Alwen in Wales had entered a swift stream-like overflow from a set of salmon-keeping tanks, in which large mature females were being stored. It is suggested that mature male parr are more active than other parr and show different migrational movements; they may also be attracted chemotactically to the mature females.

321. Hartley, G. W. (1939). "Salmon caught in the sea—the island of Soay and Ardnamurchan, 1938." Fisheries, Scotland, Salmon Fish., 1939, No. 1: 1–16. (Edinburgh: H.M. Stationery Office. Price 9*d*.)

Fish were weighed and measured by a new, quicker method, using a board and canvas pocket. Ardnamurchan smolts were the biggest yet found on the west coast. They differ from Soay smolts and have different migration routes.

322. Tulloch, J. B. G. (1938). "Insects and other things which arrive by steamer from overseas." Entomologist, 72: 114–16.

A list of Arthropoda found in banana crates from Brazil and brought to Stepney Borough Museum, 1937.

323. Dannreuther, T. (1939). "Migration records, 1938." Entomologist, 72: 119–22.

Includes table of estimates of district abundance during 1938, also additional records.

324. Dannreuther, T. (1939). "Migration records, 1938." Entomologist, 72: 9–15.

A summary of the movements of migratory Lepidoptera recorded in 1938 in the British Isles, followed by some Continental observations and a general summary of records of abundance with dates of first and last appearances.

325. Garrett, F. C. & Harrison, J. W. Heslop (1939). "Is the green-veined white ever an immigrant?" Vasculum, 25: 33–4.

Discusses evidence for and against migration of this butterfly.

326. Williams, C. B. (1939). "The migrations of the cabbage white butterfly (*Pieris brassicae*)." 7th Int. Kongr. Ent., Berlin, 1938, Verhandl., 1: 482–93.

The cabbage white butterfly is a regular migrant, the most conspicuous movement in Europe being in a southerly direction through central Europe. These flights must originate somewhere to the north of this, but so far there is no clue to the exact area, or areas, from which they come. Outbreaks of caterpillars have been recorded at times in Southern Scandinavia doing severe damage to Cruciferae, but no one has yet recorded any directional movement of adults.

327. Harrison, J. W. Heslop (1939). "*Argynnis aglaia* and *Pieris napi* flying out to sea." Entomologist, 72: 59.

Records observations on Rhum and Longay. Some of the fritillary butterflies soon returned to land, but a few sped far across the water and were lost to view. The green-veined white, however, invariably returned to the cove, or rockledge, supporting its food-plant. The possible bearing of these observations on statements concerning alleged immigrations of this butterfly is deliberately left for "consideration and appreciation of others".

328. Wakely, S. (1939). "Notes on *Pyrausta nubilalis*, Hubn." Ent. Rec. 51: 3–5.

This moth, known in America as the European corn borer, has always been considered to be a casual immigrant as far as Britain is concerned. A small colony appears to have established itself at Benfleet, Essex, on *Artemisia vulgaris*, its chief host-plant in Belgium and N. France.

329. Harrison, J. W. Heslop (1939). "The northward advance of *Plusia moneta* L." Vasculum, 25: 31.

This moth has now reached Rhum, but searches for it on the neighbouring islands of Eigg and Muck were profitless. See also **F. C. Garrett,** 1938, Vasculum, 24: 115; **J. W. Harrison,** 1938, Vasculum, 24: 101–2.

330. Daniels, E. T. (1939). "*Limnophilus affinis* Curt. (Trichoptera): an immigrant?" Entomologist, 72: 46–7.

Circumstantial evidence that an immigration of this caddis fly may have taken place at Great Yarmouth on 11 October 1937.

331. Waterston, A. R. (1939). "Migratory locust in Scotland." Scot. Nat.: 48.

An immigrant female *Locusta migratoria*, belonging to the solitary phase, was found on the island of Rousay, Orkney, in 1938. Locusts normally migrate during the social phase of their life-cycle.

332. Davies, W. M. & Whitehead, T. (1938). "Studies on aphides infesting the potato crop. VI. Aphis infestation of isolated plants." Ann. Appl. Biol. 25: 122–42.

Investigations to ascertain the extent of the migrations of winged aphides, their ability to detect individual plants, the development of aphis population following colonization, and the extent to which virus diseases may be transmitted to isolated plants by winged aphides.

333. Moon, H. P. (1939). "Movements of the invertebrate fauna over the substratum." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 41–3.

Data on the rate at which animals of the stream bed re-colonize bare stones.

334. Macleod, J. (1938). "The tick problem." Vet. Rec. 50: 1245–50.

In areas where the British sheep tick, *Ixodes ricinus*, has been long established, there is no consistent trend of increase or decrease, and the tick population level fluctuates about a constant value. The invasion of new territory often gives the impression of great increase, but on account of the relatively small areas invaded, this phase of the problem is of little importance. Spread is almost entirely effected by hosts, and the survival of ticks in new territories is largely controlled by microclimatic factors, of which humidity is the most important. Recent extension of tick territories is due to the development of favourable vegetational conditions away from cultivated types and towards a heath or moor type. Sheep dips, particularly those of vegetable origin, are useful means of prevention of tick invasion, but control will lie in the correct management of pastures marginal to tick territories. The recent movement to exterminate deer as tick carriers in certain areas is of negligible value as a control measure, since the density of deer is too low to be effective in tick spread, and the habits of deer are such that their ticks are not scattered widely, as is the case with sheep.

335. Small, T. (1939). "On the first outbreaks of potato eelworm (*Heterodera schachtii*, Schmidt) in Jersey." J. Helminth. 17: 39–40.

Tests indicated that Jersey was entirely free of this parasite in 1935 and all potatoes entering the Island since then have been certified free of the pest. In 1938 an outbreak was reported from four small potato areas and later among tomatoes. Infection is heavy and appears to be several years old. It may be necessary to use systematic crop rotation to eradicate the pest.

8. REPORTS OF ORGANIZATIONS

336. Lancashire and Cheshire Fauna Committee (1939). Twenty-fourth Annual Report and Report of the Recorders for 1937. 30 pp.

Notes on birds and Lepidoptera, some of which contain ecological information. There are special reports on the red-backed shrike (*Lanius colusio*), the magpie (*Pica pica*), the coot (*Fulica atra*), and the chiffchaff (*Phylloscopus collybita*).

337. Bureau of Animal Population, Oxford University (1938). Annual Report, 1937–8. 36 pp.

The introduction includes a classification of the factors of reproduction and mortality in relation to population dynamics, and a review of the general organization of research required for population investigations. Separate sections summarize work on vole populations, game-birds and rabbits, enquiries into North American wild life cycles, and the results of some other surveys in Great Britain. There is a list of periodicals added to the library, mostly dealing with wild life conservation and allied subjects. It is announced that the Bureau is making translations of some Russian ecological papers, copies of which can be obtained from the Bureau.

338. British Trust for Ornithology (1939). Fifth Report, Spring, 1939. 33 pp.

Reports are given in some detail of recent co-operative enquiries. The lapwing (*Vanellus vanellus*) habitat enquiry. Inquiry into the distribution of the corn-crake (*Crex crex*): 1200 returns and 1000 other communications show a general decrease, less marked in Scotland. A certain number of isolated increases are reported. The inquiry is being continued. Survey of breeding colonies of the black-headed gull (*Larus ridibundus*): the most striking fact is the colonization that has taken place inland during the last 25 years. Coastal colonization has also gone on in the west. Song period enquiry, which is being continued. Sample census of heronries. Bridled guillemot (*Uria aalge*) enquiry. Local distribution and habitat enquiries. Woodcock (*Scolopax rusticola*) enquiry. Woodland bird enquiry: it is noted that many of the special British forms of birds (21 out of 37) are woodland inhabitants. Lists are given illustrating this. Fulmar (*Fulmarus glacialis*) enquiry: figures are given showing details of the fulmar's spread since 1878, when the first colony apart from St Kilda was founded. New enquiries are being undertaken, one into the status of the redshank (*Tringa totanus*) and another into hatching and fledging periods. (For fuller notices on some published enquiries see **203, 296**.)

339. Skokholm Bird Observatory (1938). Report for 1938. 22 pp. (Address: Skokholm Bird Observatory, Dale, Haverfordwest, Pembrokeshire, Wales.)

Some of the most interesting information concerns the attempts to exterminate the wild rabbit (*Oryctolagus cuniculus*). After a last attempt to infect them with myxomatosis, which again failed to spread, cyanogas was used from November to the end of February with promising results. The house mouse (*Mus musculus*) is approaching a peak in its numbers, to which it has gradually been rising since 1935. One further experiment in homing was undertaken, a manx shearwater (*Puffinus p. puffinus*) being released at Le Havre on 16 April, and recorded back in its burrow on 15 May. There is a brief summary of the course of bird migrations with notes on weather conditions, and a number of notes on particular species. 3685 shear-waters were ringed; three ringed as nestlings in 1937 were recovered in July and August, 1938, showing that first year birds visit the colony, but do not breed. One shearwater ring has been found in the stomach of an angler fish (*Lophius piscatorius*).

340. Freshwater Biological Association of the British Empire (1939). Seventh Annual Report for the year ending 31 March 1939. 97 pp. Price (to non-members), 1*s.* 6*d.* (Address: Wray Castle, Ambleside, Westmorland.)

The work of the Association, with its headquarters at Wray Castle on Lake Windermere, is described, with particular emphasis on the relation of pure research to problems of water supply and fisheries. A new departure is the study of the bacteriology of freshwaters. The report includes six semi-popular articles by various members of the staff on the work now in progress. The first two refer to the algal cycle and its controlling factors. M. Rosenberg: "Changes in the phytoplankton". C. H. Mortimer: "Changes in physical and chemical variables". C. B. Taylor: "Bacteria in freshwaters". C. H. Mortimer: "Lake deposits". T. T. Macan & H. B. N. Hynes: "Faunistic studies". E. B. Worthington & G. H. Swynnerton: "The growth of brown trout".

341. Avon Biological Research (1939). Annual Report No. 6, 1937–8. 67 pp. (University College, Southampton. Price 2*s.* 6*d.*)

Contains a general account of the activities of the freshwater station at Southampton during the year. They included trapping smolts, experimental rearing of smolts, hatching and stocking experiments and work on the general ecology of the Avon. There are nine more detailed reports on work in progress.

342. Yorkshire Fishery District, Board of Conservators (1939). Seventy-second Annual Report on the Salmon, Trout and Freshwater Fisheries in Yorkshire. (By **W. T. Clarke.**) 43 pp.

Gives figures for the annual catch in 1938 by nets and rods in sea, estuary and river of salmon (721 fish weighing 10,964 lb.) and migratory trout (1561 fish weighing 5529 lb.), a decrease of some 70% on the previous year. Notes on brown trout and other freshwater fishes, fish passes to enable migrating fish to surmount obstructions, the Keld Head hatchery and re-stocking operations, and pollution.

343. Scottish Marine Biological Association (1938). Annual Report, 1937–8. 23 pp.

Short accounts of the work on herring, plankton, lobsters, molluscan ecology and shell formation in the crab *Carcinus maenas* are given. A list of marine nematodes from the Clyde Sea Area includes habitat notes.

NOTICE TO CONTRIBUTORS

If contributors will study these notes, they can save themselves and the editors a great deal of unnecessary work in the revision of manuscripts.

1. **The Journal of Animal Ecology** is published for the British Ecological Society, by the Cambridge University Press, in May and November each year. MSS go to press three months before they are published, and must be submitted well in advance of the date of going to press.

2. All communications should be addressed to: **The Editor, Journal of Animal Ecology, Bureau of Animal Population, University Museum, Oxford.**

3. **Text.** MSS should be typewritten, double-spaced, on one side only of the paper. Latin names of genera and species, but nothing else, should be underlined. Arabic, and not Roman, numerals should be used. For months, use abbreviations (Sept. etc.) not figures. All graphs must have corresponding tables giving the figures on which they are based.

4. **Text-figures.** Drawings should be made with jet black Indian ink on Bristol board or smooth paper, and must not be folded for postage. Allow for considerable reduction in large figures. Mark all letters and figures lightly in pencil. Graphs should be drawn on paper ruled in pale blue or light grey.

5. **Photographs.** Good glossy half-plate prints are required for making plates. On the back of each print write the number and author's name, referring the numbers to a separate sheet of titles. Number photos separately from the text-figures. Please send a selection of photographs for the editors to choose from.

6. **References.** These should follow the usage of the *World List of Scientific Periodicals*, 1934 edition, except that capitals and not small letters should be used for adjectives in the names of periodicals. All references must be verified from the original source before the MS is sent in; any not personally seen and checked should be marked with an asterisk. **Do not underline anything except Latin names of genera and species.** Please follow carefully this form of reference:

> 3. Myers, J. G. (1935). "Epizootics among fishes and reptiles on the Amazon and Orinoco." J. Anim. Ecol. 4: 17–21.

If preferred, author's name and date may be used, instead of reference number; and titles of papers may be omitted if desired.

7. **Tables and Latin names.** So far as possible put tables on separate sheets. Additions, percentages, etc., should be carefully checked. Latin names of invertebrates or of non-British vertebrates should have species authorities when the names are first mentioned in the text, or in the main tables. The Latin names must be verified either from a standard list or by submitting the final MS to the experts who have supplied the identifications.

8. **Proofs.** Page proofs only will be sent. Authors can contribute towards the economical running of the Journal by sending in MSS in final condition, and by making the minimum alterations to their proof-sheets.

9. **Reprints.** 50 reprints of each paper are given free to authors. These are sent out about a month after publication. Additional reprints may be purchased: they should be ordered when proofs are returned. Contributors from abroad should send their order with their MS.